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ABSTRACT

"Science as a Way of Knowing" is a project of the education committee of the American Society of Zoologists and 11 other organizations. The goal of the project is to offer suggestions for making the teaching of biology at the college and university level more effective. Each year the project focuses on an important subfield of biology and: (1) sponsors a symposium on the topic area; (2) develops a film program; (3) publishes an essay with an extensive bibliography; and (4) publishes the symposium proceedings. The proceedings of the 1984 symposium on evolutionary biology are presented in this document. Articles included are: "Science as a Way of Knowning--Evolutionary Biology: Opening Remarks" and "Science as a Way of Knowing--Evolutionary Biology" (John A. Moore); "The Arrogance of Ignorance-Ingoring the Ubiquitous" (William V. Mayer); "The Shame of Science Education" (E. Peter Volpe); "Science as a Way of Knowing-Evolution: The Biology of Whole Organisms" (Marvalee H. Wake); "Science as a Way of Knowing-Molecular Evolution" (Bruce R. Levin); and "Films, Filmstrips, and Videotapes in Evolutionary biology" (Nathan H. Hart). (JN)

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SCIENCE AS A WAY OF KNOWING

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An Ongoing Project of the
Education Committee
of the
American Society of Zoologists

Co-sponsored by

The American Society of Naturalists
The Society for the Study of Evolution
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The American Institute of Biological Sciences
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The National Association of Biology Teachers
The Society for College Science Teachers
The Genetics Society of America

I

SCIENCE AS A WAY OF KNOWING—EVOLUTIONARY BIOLOGY

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SCIENCE AS A WAY OF KNOWING—EVOLUTIONARY BIOLOGY

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* The talk presented by Stephen Jay Gould entitled "Paleontology and geology" was part of the Symposium program, but is not included in this volume.

AMER. ZOOL., 24:421–422 (1984)

Science as a Way of Knowing—Evolutionary Biology: Opening Remarks[1]

JOHN A. MOORE

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The most serious domestic problem facing our nation is the disastrous decline in the effectiveness of its educational system that we have witnessed in the last two decades. We live in a time when civilization has come to depend less and less on brawn and more and more on brains. Today even the major component of our brawn is brains, yet we have allowed the societal system for education and acculturation to fall into serious disarray. There is a widening gap between the haves and the have-nots in the nation: those who have an effective education and those who do not. And among the industrial nations of the world there is a similar gap—with the young people of America being found more and more among the have-nots—those who do not have an education sufficient to allow America to maintain its preeminent position in the world. This gap has important consequences not only for the health of the nation but for the aspirations of those who can not participate fully in, or receive the benefits of, our generally prosperous society.

The probable causes for this unacceptable state of affairs have been explored and debated endlessly and an impressive list of scapegoats has been assembled: broken homes, racial tension, inadequate schools, incompetent teachers, drugs, abandonment of educational standards, excessive devotion to TV, abandonment of codes of ethics, lack of faith in the nation or its future, and dogged adherence to that most persistent American myth—there really is a free lunch.

Since this scapegoating has been done mainly by those in the universities, it is not surprising that higher education has failed to find a place on that long and depressing list. But let me suggest that we in higher education must bear a heavy load of guilt because it is the universities that set the level and pattern for the education we now judge to be inadequate. When we lower our standards, as we have done for the last two decades, we are demanding less of our students and they can afford not to do their best. We lower our requirements for entrance to the universities yet are dismayed that the high schools lower their standards in concert. We accept for our Schools of Education those from the lowest quartile of the university student population, take little interest in their education, and then wonder why the teachers in the schools are not meeting the educational needs of their students.

Although it is titillating to squabble over the decline and fall of American education the problem for us, here and now, is remedial activities. The Education Committee of the American Society of Zoologists proposes that we recognize that the colleges and universities are in a unique position to foster a rebirth of quality education. There is little we can do to mend the broken homes or darken the television screens but there is a very great deal that we can do to improve the way we teach biology in the universities. Any success that accrues from our efforts will not only improve the scientific enterprise itself but will expand the horizons and increase the competence for wise decisions by citizens at large and make more effective the education of those who will teach in the schools.

We start toward this goal with our project "Science as a Way of Knowing." At each Annual Meeting of our society we will provide a package of activities and materials: a film program, symposia, and printed copies of a long essay. Each year we will

[1] From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27–29 December 1983, at Philadelphia, Pennsylvania.

explore how a subfield of biology might be developed in an introductory university course. This year the topic is Evolutionary Biology. Next year it will be Human Ecology. In subsequent years we will go through the gamut of Biology: Genetics, Developmental Biology, Physiology, Cell Biology, etc. This year's package has some unavoidable omissions: we wish we could have prepared suggestions for laboratory exercises and we hope to do this next year. We must also schedule workshops and discussion groups to exchange ideas on how to do things better. Should there be other activities?

But all of this is an experiment. Eventually we have to succeed—society has given us responsibility for the teaching of the biological sciences and there is too much evidence to indicate that we are not doing it in a satisfactory manner. So if the experiment of this year does not prove effective, then we must try other approaches.

A large amount of hard work has gone into this year's program and the most useful response that you can make is to offer your advice, criticism, and support. Nevertheless my key point is this: regardless of how much work has been done by the speakers the only effective outcome is in your hands.

AMER. ZOOL., 24:423–431 (1984)

The Arrogance of Ignorance—Ignoring the Ubiquitous[1]

WILLIAM V. MAYER[2]

Professor Emeritus of Biology, University of Colorado, Boulder, Colorado, and President Emeritus, Biological Sciences Curriculum Study

SYNOPSIS. Anti-evolution, the rise of pseudo sciences, and the renewed interest in the occult, all masquerading as science, are symptomatic of the poor job that is done explicating science as a process and a way of knowing. Disciplinary teaching emphasizes fact over concept. Every science discipline should be taught with a process base pervasive from the first to the last day of the course. Science teaching needs be revamped to provide an integrated, nonredundant exposition of the discipline focussed on principles of which the theory of evolution is only one. Science must to be related both to technology and society. Teaching has to be directed to elicit the desired ends of education and not be regarded simply as a system to deliver fragments of knowledge. The participation of zoologists in delineating the discipline of science and countering pseudo science is essential. Scientists must become involved in science education and participate in updating teachers and insisting on their subject matter competence. University scientists must be concerned beyond the training of majors to provide meaningful education for nonscience majors as well. To ensure quality science education zoologists must become active in resisting incursions of scientific nonsense in science classrooms.

Arrogance comes in a variety of forms. The arrogance of great wealth, the arrogance of great power, the arrogance of great beauty, and the arrogance of a great master are bearable because they rest on an acknowledged and measurable base. The arrogance of ignorance, however, is unbearable because it is rooted in smug satisfaction with being isolated from the facts of the case. The anti-evolution plank in the platform of Christian fundamentalism is a classic example of the arrogance of know-nothings.

Those who remember Mickey Mouse acting as sorcerer's apprentice unleashing powers he could not control will appreciate the situation in which the Biological Sciences Curriculum Study (BSCS) found itself in making the conscious decision once again to introduce the word "evolution" into secondary school biology texts despite the knowledge of potential anti-evolutionist pressures. Prior to 1960 the best selling secondary school biology text did not even have the word evolution in the index and students were exposed to a biology bereft of its most critical unifying principle. H. J. Muller's dictum of "One hundred years without Darwinism are enough" struck a responsive chord when the biology books of America were being analyzed and models prepared for future use. As anticipated, the magic word that BSCS unleashed in 1960 caused the forces of anti-evolution to become reborn with a focal point for their energies.

The anti-evolution movement has grown far more sophisticated than it was at the time of the Scopes trial. With knowledge gained by successive rebuffs it no longer demands that evolution be excluded from textbooks. It has adopted, instead, a philosophy based on the "if you can't lick 'em, join 'em" thesis. Today its members claim not to be anti-evolutionists but, rather, "scientific" creationists who offer an alternative and valid scientific explanation of organismic diversity and relationship. They purport to offer an explanation of origins based on the literal interpretation of the Genesis book of the King James Bible. It is no longer banning of evolution they demand; they plead instead only for equal time and fair play for an alternative, scientific thesis. It is as if Einstein had requested equal time for relativity whenever Newtonian mechanics were to be discussed. The effect, however, is not the same, for the creationist thesis rests on no

[1] From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1983, at Philadelphia, Pennsylvania.

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valid scientific data, has no hypotheses, offers no experiments, and has no validity within the scientific realm. The demand for its inclusion whenever evolution is discussed has the effect of muting or, worse, permuting the science thus presented. Bad science can not generate valid hypotheses and does nothing to enhance science.

In the beginning, I thought that anti-evolutionists were simply mixed up epistemologically, that they did not understand the structure of knowledge, that they could not differentiate between data derived through a theological system *versus* that derived through a scientific system. I was so naive that I felt logic, reason and the facts of the case would be enough to convince people who were scientifically uninformed. I soon became disabused of the concept that this was an innocent group with which I was dealing. I found, instead, that it was a group whose reception of ideas contrary to their own was blunted by a shield of ignorance proudly borne. This has been demonstrated again in 1983 in relation to the Texas Guidelines and Proclamation 60 dealing with content of texts to be approved for use in Texas. I have testified before the Texas State Board of Education as have distinguished scientists from the University of Texas from Nobel laureates to instructors, citizens concerned with education and churchmen. The Texas State Board of Education, so far, has ignored the ubiquity of scientific evidence and has been refractory to all of this testimony.

While all the sciences support the theory of evolution, the anti-evolutionists ignore such support because they feel obligated to their foreordained conclusions. The Earth must be 10,000 years old; the Noachian flood did lay down the entire fossil record at one time; species are immutable; there is no descent with modification; and organisms are not related. Anti-evolutionists hold such theses in spite of monumental evidence to the contrary. Not only do they display the arrogance of ignorance; they have infinite capacity to ignore the ubiquity of the scientific data that support the theory of evolution.

Regardless of their professed aims their desire is to eliminate evolution, not only from the schools, but from the public mind as well. The lengths to which they will go to achieve these ends is demonstrated by Ray E. Martin in the article entitled "Reviewing and Correcting Encyclopedias." According to Martin the way to deal with the topic of evolution is by ". . . cutting out the sections . . . practical if the portions removed are not thick enough to cause damage to the spine of the book as it is opened and closed in normal use. When the sections needing correction are too thick, paste the pages together being careful not to smear portions of the book not intended for correction." The anti-evolution plea for equal time and fair play is sabotaged by their own actions of which this is just one example. Fundamentalism, with its desire to turn back the clock, has had negative effects on all societies whose policies it has influenced. Paul Gigot writing in the *Wall Street Journal* provides a quote very similar to those heard in the United States to the effect that censors "are hurting our children. They will limit their vision, limit their tolerance." In this case the quote refers to Moslem fundamentalism which is a strong political force in the government of Pakistan.

Science will not alter the mind-set of the anti-evolutionists any more than its data have changed the minds of the members of the Flat Earth Society. Our society can and does tolerate eccentrics; but should not be sympathetic when such as anti-evolutionists organize to convince the general public that their warped data and misinterpretations are based on evidence that is as scientific as that for the theory of evolution. We cannot support in classrooms or in the minds of the general public misrepresented and unsubstantiated statements masquerading as science for, like Gresham's Law in Economics, such poor data, misinterpretations, and muddled epistemology debase the scientific enterprise through confusion and delusion. Science must focus primarily on the uncommitted. Anti-evolutionists cannot be reached. Scientists do not need to be convinced. However, the non-scientific general public is uninformed on the issues and given the fair

play, equal time ploy, see no harm in including what they do not recognize as scientific nonsense in science classes.

Why should this be so? The answer is that at all educational levels we usually do an abysmal job of delineating science as a way of knowing. Our students do not understand the validity of data derived through a scientific process compared with that derived through processes of social sciences, the humanities, or theology. They cannot differentiate between a scientific observation and a theological belief. We have given them no guidelines by which the credibility of data in a given situation can be measured. We have students who can define an adambulacral ossicle, but we also have graduate students and, unfortunately, some members of the faculty who cannot define science. If its practioners do not understand the art they practice, how can those who are not conversant with the field be held to understand it?

We are all familiar with the textbook that begins with a chapter on "the scientific method" which goes through a cookbook sequence of truisms that will lead to correct answers if properly applied. Fortunately for the understanding of the scientific process this material is forgotten after the first chapter and never again referred to. We have textbooks at both the collegiate and secondary levels that do not even include the word "theory." It does not seem unreasonable that students in a science course become familiar with such words as data, hypothesis, controlled experiment, theory, induction, deduction, observation, and similar terms that have a quite restricted and specific meaning within the field of science that does not extend to their general use. Time and again I have run across the expression in the general public that a theory is just a random guess. The State of Texas, for example, demands a statement in the front of each secondary biology book that the theory of evolution is "clearly presented as theory rather than fact." The inability to recognize the power of the synthetic explanation of a wide variety of facts that is a theory is understandable when people are not exposed to these interpretations.

It is not enough to simply introduce those terms and define them. They need be used. They need be pervasive throughout a science course. Every new conceptual scheme with which we deal should provide students the critical hypotheses on which it rests. Students should understand the data on which it is based. They should understand the credibility of its statements. We must stop teaching science as packages of facts with which the student can retreat and be assured of truth into the future. The tentative nature of science needs be discussed; otherwise we push students into a dangerous relativism when they find that the facts with which they have been provided are no longer valid. We know that the history of science is strewn with discarded theories which someone at one time held in high repute. We know that our facts change from time to time as we accumulate more information. Science is not dogmatic but forever changing and striving for further explanations of the natural world. That is a noble and contributory undertaking in contrast to the inflexible dogmatism of the anti-evolutionist.

If chemistry and physics and biology are sciences let us teach them as sciences. Let us teach their concepts, their data, their experiments, and their implications for science and society at-large instead of simply presenting formulae and vocabulary to be memorized in incessant sequence while omitting the conceptual base of the discipline. One of the things each of us as scientists should strive for is communicating the nature of the discipline. We have certainly not done very well when you look at the bookshelves in student bookstores and see the tremendous number of pseudo scientific paperbacks passed off as apparently valid science. Von Daniken, Velikovsky, the works of anti-evolutionists, materials on the occult such as the *Amityville Horror*, and other similar volumes, which many take at face value because they have not been given a standard against which to measure such material, all sit on shelves cheek by jowl with science paperbacks. The public has no way of determining that Von Daniken's *Chariots of the Gods* is not equally as valid as the *Double Helix*. They are unable to dis-

tinguish between pyramid power and nuclear power. Practically every major newspaper in the United States daily runs a column on astrology, but there is no corresponding column on astronomy even once a month. Among our more popular pseudo scientists are food faddists with their quack diets of black strap molasses and yogurt or other quack health remedies. Some still seek sources of laetrile which has no value whatsoever. People wonder why, if we can put a man on the moon we cannot do something else without realizing that the scientific requirements for putting a man on the moon are quite different than solving societal ills from a social standpoint. Science is poorly understood as a discipline and it makes small effort as a discipline to explicate itself to the general public, let alone its own practitioners.

My first plea, therefore, is to deal with the discipline of science. Deal with science as a process. Make sure that no student taking a science class completes the course without a comprehension of what it is science does, how it is science operates, and the validity of the conclusions reached by scientific mechanisms. Give students an appreciation of science as a standard against which to measure the nonsense pedalled to the public as science.

My second plea is that we go from the general to the specific, integrating our science and avoiding duplication. Currently we present science fractured into a series of independent disciplines to the point where we concentrate on individual trees and the students never see the forest. We speak of the discipline of biology, but we still have many institutions in which students cannot get a degree in the subject. Instead, they take courses in zoology where they learn about the cell, and mitosis and how to use the microscope; they take courses in botany where they learn about the cell, and mitosis and how to use the microscope and they take courses in microbiology where they learn about the cell and amitosis and how to use the microscope. This redundancy, our capacity incessantly to circle a relatively small number of content points at higher and higher vocabulary levels, does much to turn students from science.

Where we developed the concept that first one must have all of the details in place and all of the words defined before one can think properly about a topic I do not know. It is not a procedure we follow in any other field. Politics, for example, seems to demand exactly the opposite set of skills. There is no reason why one could not start with the theory of evolution and, having established its ubiquity, then derive the data on which it rests. Is organismal phylogeny a prerequisite to understanding evolution, or does a comprehension of evolution make organismic phylogeny comprehensible?

Students should be well versed in the big biological ideas and comprehend theories and their applications throughout the field of biology. The germ theory of disease, the chromosome theory of inheritance, and, of course, with primacy above all of these, the theory of evolution—all should be referred to wherever applicable in the course of a year's work and related to and substantiated by the subject matter of a given presentation, whether it be physiological, morphological, genetic, or ecological. Evolution must be the structural element of biology through which all other data become related and explicable. John Moore's essay has given us a guideline when he states "we must accept that everything cannot be covered so the emphasis must be on the ubiquitous and important and not on the rare and important or ubiquitous and unimportant."

We must discontinue teaching science as if it is a self-contained discipline existing of, by, and for itself. Instead we must begin to understand and to communicate the relationships between science, technology, and society. We must acquaint students with the applications of science to their everyday lives. We must refute the image of a scientist as one who makes monsters in the basement or unleashes deadly radiation or chemicals upon an unsuspecting population. Scientists are normally regarded as detached and concerned with other than human issues. In treating science as an enterprise that exists for itself, we have

failed to relate science to the human mainstream. Students, particularly non-science students, must become acquainted with the societal applications of science and the fact that scientists are as concerned with society and humanity as anyone. We are always greatly involved with the training of our majors, but a major in science does not present as many problems as a non-major in science. There are more non-majors than majors. Most voters are non-scientists and their misunderstanding of science is abyssal. This is a situation that need be remedied.

In most universities with which I am familiar, the introductory biology program, and particularly if it is for non-majors, is usually assigned to the newest, most junior member of the department who ultimately plans to teach upper division or graduate courses as soon as he can be released from the onerous freshman chore. I submit to you that it should be exactly the opposite. The non-major course should involve the finest minds in the department and should represent a spectrum of science that will impact significantly on those who will take no more science. We cannot wait for a graduate course in evolution to explain evolutionary theory. It must be explained at the introductory level instead of the plethora of useless names and detail that usually occupies the freshman course. There have been some notable exceptions to this observation, but they are too few and far between to ensure that the non-scientists in our colleges and universities have anything like a comprehension of the discipline.

We deprecate the inability of students to read well, to write or to speak well, to think critically, to reason, to analyze, to synthesize, and to evaluate. But why should we be surprised when we do not teach for these ends? Again and again in discussing objectives with educators, I find that their major objective is to create a student who is an independent learner and a rational and critical thinker. But we teach as if dependence were the rule, not independence. We make it impossible for a student to learn outside the classroom. Our programs are geared to criteria which require the student to attend a certain number of classroom lectures, complete certain numbers of classroom examinations, certain numbers of readings, certain numbers of laboratory experiments, and when those are done under our supervision the student then can be pronounced conversant with the topic. Our technique actually prevents the very thing that we declare we wish to do. Basically the bulk of American education in 1980 is similar to the bulk of American education in 1930. We have achieved fifty years of non-progress in education. As a meaningful innovation imagine a university not broken into traditional departments but rather organized around great concepts. A sort of Mortimer Adler's Great Books doing for science what he attempted for all knowledge. What if our teaching programs were ordered around topics such as energy, evolution, development, environment, inheritance and the cell instead of mammalian anatomy, physiology and taxonomy? The prospect for new syntheses and conceptual learning would be greatly enhanced.

It should not come as any shock that we are a scientifically illiterate society. Half of the population makes its acquaintance with science in the elementary and secondary schools and most of the other half receives a quick survey in an introductory collegiate course. It is these courses on which we need to concentrate to alleviate the scientific ignorance of our population and it would not, incidentally, hurt to have those who major in science understand more about it as a discipline and as a way of knowing. The arrogance of ignorance is everywhere apparent. Decisions are being made loudly and clearly on inadequate and inaccurate data. The proponents of certain theses seem almost proud of the fact that they are not influenced by the realities of the situation. When all around us we can see the necessity for scientific knowledge and for a comprehension of the relationship between science, society and technology we seem to be offering less and less in the way of such comprehension. We are ignoring the ubiquitous. We speak of an age of sci-

ence, we speak of an age of technology, we speak of necessity of a scientifically and technologically literate population and we ignore the evidence that we seem to be proceeding to exactly the opposite end.

My third plea is for the scientific community to participate more actively in countering the attacks of the know-nothings of the world and to become involved in science education at all levels. The scientific community *must* organize resistance to those who wish to remove something from a curriculum, place something in a curriculum, or change something already in a curriculum to reflect their own personal, special, non-scientific interests. This means that scientists must speak out against the anti-evolutionists, those who do not believe in the germ theory of disease, the anti-sex educationists, the anti-behaviorists, the anti-vivisectionists, those against population control, and others with special axes to grind and who want the data of science changed to reflect their personal biases.

Twenty years ago I found it very difficult to enlist the services of my scientific colleagues to counter anti-evolutionists. Most responded to my importunings with only two kinds of reaction. One was apathy. They simply did not see how anti-evolution would in any way influence their own researches or their own scientific interests. The other was incredulity. Certainly I was mistaken that a tempest was abrewing in a teapot. No thinking individual could return to the Wilberforce/Huxley era and certainly none in this enlightened age could give credence to either the immutability of species or a young earth. However, this situation has changed as the scientific community has observed the successes achieved by the anti-evolution movement through default. The fact that a state legislature would actually pass a bill giving the Genesis version of the King James Bible equal classroom time with the theory of evolution did cause some reaction within the scientific community. Practically every major scientific and educational organization in the United States is now on record as opposing the teaching of creationism as science whenever evolution is mentioned, but it is not sufficient that resolutions be passed. They are helpful, but they are like the studies that clog my files. Without active implementation they are conveniently put away and forgotten.

I also speak for active involvement of professional scientists in the field of education, and certainly within the field of science education. A couple of years ago the topic of creationism was brought up in the schools of Livermore, California. Now Livermore, as you know, is an area of high scientific technology. The Livermore Laboratories are there and there is a population of scientists and engineers who are supposedly concerned with parameters of their discipline and the scientific education of the youth of the community. It was the mothers, however, who uncovered the problem and led the fight. A pupil came home from the Livermore public schools and asked his mother if the family believed in evolution, to which his mother replied in the affirmative. The child then responded, "Well then, we can't believe in God, can we?" Investigating where this statement came from led to uncovering the fact that creationism was being taught in a public school and that students were being told that one either believed in God or atheistic evolution; but could not possibly believe in both. It was the mothers of the region who led the fight to remove this dogma from the public schools of Livermore. If this type of thing can happen in a high-technology scientifically oriented community, think of its impact in areas less sophisticated in scientific matters.

The history of American science education is one of lurching from crisis to catastrophe. In the late 1950s the Soviet Union did American education a great favor by launching Sputnik before our own space efforts were off the ground. It is not quite fair, however, to indicate that the entire educational reform movement of the 60s was a direct result of the Soviet's Sputnik. Prior to that time there had been periodic concerns about the quality of American education in science and mathematics and some curriculum reform projects were underway. Sputnik may have accelerated this concern but already in pre-Sputnik

days, work was being done to alleviate it. I use "work" in the sense of something being actually accomplished. Mostly we study a problem to death. I have filing cabinets full of studies which reiterate the same theses over time. In 1960 Paul DeHart Hurd published a book entitled *Biological Education in American Secondary Schools—1890–1960* which demonstrated that there was nothing new under the sun. Commissions and study groups since 1890 had been meeting and making recommendations that were simply not implemented. Today, in 1983, we are still producing reports about the state of education in the United States with no plans for implementation of their recommendations.

The one golden moment in American education that resulted in action not words was the curriculum development movement of the late 1950s and early 1960s. Funds were made available through the National Science Foundation to groups of scientists and educators to revise secondary school curricula to bring them in line with the cutting edge of disciplinary knowledge. The CHEM study, the Chemical Bond Approach, PSSC physics, and a variety of mathematics programs, in addition to the programs of the Biological Sciences Curriculum Study, resulted in books that have had a lasting impact on secondary science education. The products of these studies were not intended as an end in themselves but simply as models of what should be, and it can be said without fear of contradiction, that no secondary science book in the 1980s has been uninfluenced by the work of these curriculum groups.

However, today, in 1983, we face another crisis in science education. Were the curriculum development activities of the 1960s a failure? The answer is "No." They were a step in the right direction but they dealt basically with one facet of science education, namely textbooks which they dragged kicking and screaming into the 20th Century. However, this effort can be likened to running a 90-yard dash—an event for which no award is given. Concurrently with the appearance of new textbooks, the National Science Foundation undertook what was initially a program to up-grade teachers of science who had not returned to the classroom for a decade or more. However, there was little coordination between the curriculum materials produced and the teacher preparation activities that ensued. As a matter of fact, NSF went out of its way to avoid promoting what it regarded as its own wares. The result was that one branch of NSF put money into the preparation of new science materials while another branch prepared teachers, but not necessarily in the NSF sponsored curriculum materials.

The educational establishment is a complex of interactions among textbooks, teacher preparation, colleges of education, standardized examinations and the multiplicity of school districts in the United States, each with its own objectives and each with its own priorities. Paul Hurd has compared education to a multi-billion dollar corporation with 17,000 Boards of Directors. The argument between centralized *versus* diversified control of schools is one that has involved every segment of our society with proponents on both sides pleading on the one hand for unity, on the other hand for diversity. Intelligently handled either option can lead to successful educational practices. Without intelligent leadership neither is worth considering. Unfortunately, mismanagement in either system has usually been interpreted as a deficiency of the system itself rather than a problem of placing blame where blame is due. Frequently the representatives of various segments of the educational continuum blame one another for lack of progress. We have a vertical column of blame. The graduate schools indicate that the undergraduate program does not properly prepare students for graduate work. The upper division of a college or university blames the lower division for the lack of preparation of its students. Those in charge of freshman courses blame their lack of success on the secondary schools. And then, in turn, the blame cascades down to junior high schools and elementary schools and kindergarten and preschools. None of which, apparently, is doing the proper job of educating for those more elevated in the hierarchy.

In addition, there is a horizontal plateau of blame. The teachers blame the parents and the home environment. The parents, in turn, put the blame at the door of the teachers. The textbook becomes a matter of controversy. If we had better and more modern texts, we could do a better job; or the textbooks we have incorporate values that are better dealt with in the home environment. Teachers blame administrators; administrators blame teachers. Colleges of education, when called to account for the quality of their graduates, blame their problems on the liberal arts colleges. They say, in essence, that their students get their subject matter backgrounds from colleges of liberal arts and that education colleges really have them for a very short period of time, so they cannot be blamed for their lack of ability. However, no concerted effort has been undertaken to prepare teachers properly in subject matter. Most subject matter departments make no concession to the tasks of the teacher, and most courses are not applicable to the problems with which the teacher will have to deal. How many introductory biology courses, for example, devote any significant time to the theory of evolution and its place within biology? How many biology majors have ever had a course in evolution? How many universities even offer such a course? The training of teachers is done poorly. Colleges of education devote little time to subject matter, but instead, concentrate on what they term the art of pedagogy.

All kinds of requirements have superceded classroom competence. Unionized school districts allow seniority to be a governing factor in retention and promotion. A superior science teacher with 10 years of service might find his place taken by a home economics teacher with 15 years of service. These lateral arabesques do education no good and place teachers not competent to deal with the content of the discipline under consideration in front of classes. Actually, the number of teachers properly certificated to deal with science is far less than 100% and growing smaller all the time. Today, an art teacher may be handling sections in science. Until we are capable of placing properly prepared teachers in science classrooms, science teaching will suffer. With many collegiate departments being reduced in size or eliminated entirely, there has been a move at the college level to perform similar lateral arabesques with the thesis being that a person with a Ph.D. in a subject matter should be able to transfer laterally into another field because of innate competence in knowledge and the art of teaching. So far this has not gotten very far in the university system although some junior colleges and some small colleges have transferred professorial personnel across the disciplines. It seems odd that in the field of higher education where teaching competence has not normally been a criterion for hiring, retention, or promotion, that one would be able to make the case that there is a teaching art transferrable from one discipline to the other.

Our educational system is frequently a placebo system. We avoid controversial issues simply because they lead to contention. But education demands we deal with controversial topics; not indoctrination, but education. The line is thin, but it can be walked. To avoid the teaching of evolution because it induces problems is to avoid educational responsibility. Evolution is the warp and woof of biology as the atomic theory is for chemistry. Biology no more makes sense without the unifying conceptual scheme of evolution than the elements could be ordered without an understanding of atomic theory. The implications of evolution for human welfare and undertakings is well documented in the accompanying essay of John Moore (1984). Teachers in the public schools are particularly intimidated by the teaching of evolution for the anti-evolutionists have been active on the local front. They spend their time dealing with all facets of the educational continuum; they importune legislatures for equal time laws, which is perhaps their least successful activity but one that is highly visible and garners them the publicity they so need for continuing fund appeals. They have had better success with state boards of education. The Texas Board of Education, for example, has bought the

anti-evolutionist arguments lock, stock, and barrel while, at the same time, disclaiming that any anti-evolutionist input has been involved. The intellectual gymnastics required to implement anti-evolutionist dogma while denying that it has any influence on the actions taken is a wonderful sight to behold at a Board of Education meeting.

The anti-evolutionists importune school administrators, local school boards, and individual teachers to eliminate, mute, or misrepresent evolutionary theory or to turn science classes into Sunday School classes by the demand that Genesis be given equal billing whenever the theory of evolution is mentioned. Teachers who have a hundred and fifty students a day in five different classes are not looking for further divisive activities of a contentious nature. When badgered by anti-evolutionists they normally capitulate. They solve their problem by falling completely into the anti-evolutionary trap by simply not teaching evolution. This way they avoid the possibility of extended contentious confrontations. As evolution was never a major part of their biological coverage in the first place, they feel its elimination is no great loss and a small price to pay for community peace and quiet. Thus, the anti-evolutionists, by simply threatening to demand hearings or bring legal actions, force the elimination of evolution from the curriculum without a shot being fired. Not every teacher wants to be a John Scopes. They have neither the heart nor the mind for the task.

In summary, what we need is sustained federal interest in quality education. We need updated, non-redundant curricula that reflect the current state of the discipline and integrate it with other disciplines as well as the daily lives of our students. We need teacher education programs that will update those teachers who have not had a class in science for a decade or so. We need colleges of education that ensure subject matter competence for teachers as well as pedagogical competence. We need a coordinated effort to improve the quality of science instruction. To this end we need untainted textbooks—ones that present the conceptual basis of the discipline without bias. We need the processes of science to pervade both our books and our classes. We need to eliminate the practice of placing non-qualified teachers in front of classes simply because of their longevity within a given system. If teachers are to make lateral arabesques in their career this should not be done until they have had a chance to be prepared in the subject they are asked to teach.

And lastly, we need the cooperation and involvement of the entire scientific community to take a stand for quality education and to resist the incursions of non-scientific nonsense masquerading as science. We cannot tolerate the arrogance of ignorance nor ignore the ubiquity of scientific concepts in our daily lives. We must all strive for the achievement of scientific literacy. It is the job of each and every one of us to insist that science education is modern, accurate, and comprehensible and to ensure that, while there may be non-science majors, there are none who remain unacquainted with untainted science.

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The Shame of Science Education[1]

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SYNOPSIS. Public understanding of science is appalling. The major contributor to society's stunning ignorance of science has been our educational system. The inability of students to appreciate the scope, meaning, and limitations of science reflects our conventional lecture-oriented curriculum with its emphasis on passive learning. The student's traditional role is that of a passive note-taker and regurgitator of factual information. What is urgently needed is an educational program in which the students become interested in actively knowing, rather than passively believing. The use of problem-based learning provides a rich vehicle for making our students active participants in the learning process. One of the most effective ways of implementing problem-based learning is to organize the students in small discussion groups. The potential of small, carefully structured learning groups in higher education has yet to be realized.

The public continues to be naive and unconversant with the limits and accomplishments of science. The vast majority of individuals in our society know little about science and do not, at least consciously or obviously, seem embarrassed by being uninformed. When the average person does express an interest in scientific developments, he or she frequently dwells on the exotic and the bizarre. Even more alarming is the general willingness of the public to accept the irresponsible exaggerations of the news media and press.

We may examine a recent episode. In 1978, the free-lance writer David Rorvik, promoted his book entitled *In His Image: The Cloning of a Man.* In this book, Rorvik made the extravagant claim that a genetically identical replica, or clone, had been created of an aging millionaire. Presumably, in September 1973, a 67-year-old millionaire named "Max" asked Rorvik for help in arranging the cloning of an heir. Rorvik asserted that he introduced Max to a scientist named "Darwin," who agreed to undertake the project at a secret laboratory set up outside the United States and totally financed by the millionaire. Then, in March 1975, Darwin reportedly was able to incorporate a body cell taken from Max into a human ovum from which the nucleus had been removed. The resulting embryo was implanted in the uterus of a 16-year-old virgin who gave birth to a boy alleged to be a genetic copy of Max. Rorvik's book was rushed into print three months ahead of schedule by the publisher J. B. Lippincott, a reputable publisher, who nevertheless could not resist foisting this incredible story on the naive public.

All members of the scientific community viewed with astonishment the simple-minded readiness with which the general public and news media accepted the bold assertions by Rorvik. The popular press contributed its usual brand of exaggeration with stories of cloning that were more startling than enlightening. Any knowledgeable person familiar with the available techniques and current findings of transplantation of nuclei would have immediately dismissed Rorvik's assertion as blatantly implausible. Yet, it took a Congressional hearing and the sober testimony of several respected biologists to impress upon the average citizen that the claim of a cloned human was pure fiction and a hoax.

There is no doubt that the public's perception of science is appalling. Who is to blame for the stunning ignorance of science displayed by the average citizen? One fashionable explanation is that the newspapers serve science badly. It is probably true that the treatment of science in the press is less than satisfactory, but this is

[1] From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1983, at Philadelphia, Pennsylvania.

obviously far from a conclusive answer. It is also true that the scientific advances, in recent years, have occurred so rapidly that most people cannot digest the rush of new discoveries. The brisk output of new knowledge disturbs one's serenity. Indeed, the novel and awesome powers of modern science arouse suspicious concern. The real hazards of nuclear power and the greatly magnified risks of recombinant DNA research have tended to undermine public confidence in science. To many people, science has become a dehumanizing force in our society. It may well be that many people are rebelling not so much against science as against a world they perceive as insensitive to human values. Such rebellion may be part of a broader anti-intellectualism. Nevertheless, our universities must assume a prominent role in countervailing, or at least neutralizing, the antiscience attitude.

Tragically, the greatest culpability for the sad state of society's scientific understanding is our educational system itself. Education in the sciences is pathetically wanting. Too many students leave our lecture halls unable to reflect thoughtfully on scientific information. Yet our students will shortly find themselves within that segment of society whose views are most influential in shaping public response to scientific developments. It is important that our students be prepared to evaluate evidence dispassionately. Why is science education in such sorry shape? Some of the reasons will become apparent as we explore another recent episode.

An incredulous story unfolded in Louisiana in the summer months of 1981. For several hectic days in mid-July, educators, scientists, and thoughtful theologians earnestly entreated Governor Treen to veto a misguided bill, which mandated that the public schools of Lousiana teach the so-called theory of "scientific creationism" whenever Darwinian evolution is taught. But the voices of scholars fell on deaf ears. Scientific creationism is a perversion of both science and religion. University scientists have been justifiably perturbed by the irresponsible distortions of science habitually propagated by fundamentalist creationists. Biblical scholars have been embarrassed that religious beliefs are misrepresented by the creationists as true science. As one prudent theologian stated, the theory that God made a young earth (not more than 10,000 years old!) to look old (that is, instant antiquity!) invites the deplorable idea that God cannot be trusted.

The roots of the creationism movement spring from Protestant fundamentalism and political conservatism. The legislators and Governor Treen capitulated to the intransigent Protestant fundamentalists, who insist on the literal truth of the Bible and have a strong following in north Louisiana. The measure was authored by Senator William Keith, a Baptist divinity school graduate, who publicly stated his indignation that his children were taught that "they came from monkeys." To the creationist, any notion that humans evolved from lower forms of life is unconscionable because of the biblical account of God's special creation of Adam and Eve. To a biologist, it is utterly incomprehensible that students leaving our educational system can remain naive enough to believe that a rib from a man can be used to create a woman, or that the universe is no more than 10,000 years old. Certainly, there is a major failing in science education if our students are unable to differentiate between religious beliefs based on inflexible propositions and scientific concepts grounded in testable hypotheses. Fundamentalist creationism is not a scientific alternative to Darwinian evolution. Scientific creationism demands the absolute acceptance of views not subject to test or revision. Science necessarily rejects certainty and predicates acceptance of a concept on objective testing and the possibility of continual revision. The claims of the creationists are unverifiable (or unfalsifiable) and, hence, inherently unscientific.

The reaction of the public to the issues of scientific creationism has been largely one of confusion. The average person in the street has been baffled by the complex arguments on both sides. Creationists challenge the validity of the data supporting gradual evolutionary change, emphasizing the deficiencies in the fossil record. Evo-

lutionists acknowledge that there are uncertainties in the details of evolutionary history, but that our body of evolutionary knowledge is continually growing and increasing in accuracy. The layperson is not generally conversant with the philosophy or methodology of science and lacks the confidence to weigh the issues. The local citizen perceives the controversy as a dispute between two groups of passionately committed individuals and supposes that one outlook is as good as another. When the creationists ask for equal time in the science classroom, the person in the street views the situation as a reasonable request for fair play. This would not be disconcerting, were it not for the fact that local citizens do impact upon our educational system in many ways. Local citizens serve on boards of education, and are dragged into textbook disputes—including the rejection of texts that propound the evolutionary concept. Accordingly, our local citizens are important because their views are heard or expressed in parents' groups, board meetings, and referendums.

A major complaint of professors at colleges and universities today is that entering freshmen are uneducated, if not practically illiterate. The teaching of science to disinterested, unsophisticated students is a difficult endeavor. Beginning students enter college with vague and naive notions about evolution. They look upon evolution as something that has occurred in the remote past. They know it has something to do with dinosaurs, rocks, and the proverbial "missing link." And they are familiar with such proverbial cliches as "struggle for existence" and "survival of the fittest." But, even after a year of introductory college biology (or because of such exposure!), the average student is still disbelieving that the human species is simply an incidental and fortuitous episode in the age-long history of life. Students may acknowledge that the story of Adam and Eve is a myth, but Darwinian evolution represents a crushing blow to their preening self-esteem. It is inconceivable to many students that humans are not the unique crown of the universe. Science demeans the concern for our ultimate destiny. If we are simply an animal, how could we have an immortal soul, destined for eternal happiness (or punishment)? Many students make a point of being religious in order to avoid the fires of Hell or reincarnation in some less desirable form.

Darwinian evolution ostensibly robs human life of its mystery and melancholy. One of the most painful disappointments to the poetic or romantic mind is acceptance of the notion that life may not be eternal. A prevailing feeling is that science squeezes the beauty and warmth out of all that it touches. The remarkable advances wrought by science and technology are viewed as satisfying only our material needs—from the harnessing of steam and electricity to the development of antibiotics and vaccines. Very rarely are the achievements of science thought of as enabling men and women to have a more humane view of their fellow passengers.

Darwinian evolution does offer a new way of looking at nature and a new way of looking at life. Yet, our college students have not appreciated the potentially profound implications of Darwinism for developing a comprehensive view of human nature. The students, however, have assimilated the precepts of art, music, literature, and philosophy—all of which have strong elements of religious intuition or of mystic communion. The humanities—not the sciences—make students feel more humane. The humanities are the disciplines that express concern for the human individual.

The college freshman stands with one foot in the twentieth century and the other in the thirteenth century. The resultant straddle between science and superstition is both painful and embarrassing. Some students attempt a reconciliation or fusion of the two ideologies: naturalistic and mystic. For many students, the mystic conviction is overwhelming and primary, overriding any consideration of objective science. In fact, students are drawn to the occult, the supernatural, and the paranormal. It is as if they crave to learn the secrets of their "psychic souls." The students delve into movies, books, magazines, and cassettes dealing with subjects ranging from astrology to witchcraft. Occultism has been promoted by the popular media. Even

though occult or illusory beliefs are objectively unsupportable, many students uncritically endorse the fanciful. Apparently, the need to retain irrational beliefs satisfies personal needs that seem to be denied by modern science and technology.

There is an important lesson to be learned: Science, evidently, is not viewed by students as a way of reaching a deeper understanding of ourselves or of our environment. Science, unlike the occult, is not apprehended intuitively by the students. Science is, at best, a dry technical methodology, with its antiseptic habits of close analysis. It is cold and impersonal. The study of science is alienated from the life of the student. The agonizing feature of science education today is the wide gulf between one's studies and one's life. The challenge of education in the sciences is to expose students to learning experiences that will make the scientific outlook part of their daily living. The challenge is to offer the student a curriculum in which learning and living can be integrated. The student must experience learning. Changes in skills and judgment occur when the student lives through an event or events.

The insensitivity or indifference of the students to science reflects our traditional curriculum with its emphasis on passive learning. The student's traditional role is that of a passive note-taker and regurgitator of bits of facts. From kindergarten on, students have been exposed to a model of learning in which the teacher decides what information the student should learn, how it is to be learned, in what sequence, and at what pace. The paramount feature that identifies a teacher-centered curriculum is that the student is not responsible for his or her own education. The student's task is to copy a steady stream of words in a formal lecture and to repeat the information parrot-like on command. The students are so preoccupied with transcribing the gospel-like offerings of a lecture that they scarcely have time to ask questions. The rewards to the student in a teacher-centered curriculum are usually external, as motivation is based primarily on grades and not on a personal desire for achievement.

Let us consider the full implications of a teacher-centered curriculum. The vast bulk of students who will take freshmen college biology—fully seven-eighths of them—will never enter the door of a biology classroom again. Yet, all too often the liberal arts nonscience major is exposed to a highly factual, encyclopedic introductory course in biology. The course is frequently an introduction to advanced courses for the science major that the nonscience student will never take. Rarely does the student experience the intellectual excitement involved in the search for knowledge, or sense the fervor in scientific inquiry. Lost in the lecture process is any participatory probing by the students. The passive role of the student contrasts sharply with the active role of the teacher. The teacher's activity promotes learning—for the teacher, not for the student! By and large, the teacher feeds information to the students as a finished product, and does not reveal his or her own creative efforts in weaving the material in finished form. Teachers feed students complete meals, to borrow an analogy from Robert Marcus, provost of Rollins College. The teacher does not generally invite the students into the kitchen to witness all the crucial ingredients and manifold steps used to prepare the final fare presented to the students in the dining room (or classroom). We should be able to devise an instructional program around the precept that we make available to our students the skills in learning that we possess but which the students have not yet acquired.

Evaluation procedures are necessary to assess student progress and competence. Unhappily, evaluation is usually accomplished by the wrong approach: stereotyped, standardized, non-educational examinations. For students, past schooling has equated education with objective-type examinations, and the colleges reinforce that view. Faculty members remain complacent in their ignorance of the pitfalls of standardized examinations and the students suffer. A standardized examination of a multiple-choice format usually places stress on simple recall of information. It is safe to say that objective-type examinations

do not properly test competence in the sciences. Multiple-choice-type examinations glorify facts; indeed, only an expert in the given speciality can answer many of the trivial questions. Most knowledgeable educators contend that a standardized examination measures only how well a student has studied for the examination.

We may well ask: Are there any redeeming features in a teacher-centered curriculum? Presumably a primary goal in a teacher-centered curriculum is to transmit an organized body of knowledge. It is assumed that when a student has amassed a large body of knowledge, he or she is prepared to apply that knowledge to the solution of problems in everyday life. Ironically, the student is given a problem to solve after he or she has been provided with the facts. But this is contrary to what occurs in real life. In our daily lives, we face many problems, and learning occurs as we work toward an understanding or resolution of the problem. Thus, in the daily learning process, the problem is encountered first. In the education of our students, should not the problem be given to the student first?

The use of problem-based learning provides a rich vehicle for making our students active participants in the learning process. It is fruitless to have a vast store of information without a method of ordering the information. The body of factual knowledge in science becomes meaningful when it is used in the solution of a problem. Students acquire knowledge in relation to the resolution of problems. The assumption of sequential learning is challenged by the problem-solving approach. In evolutionary biology, for example, it is not necessary to learn the evidences of evolution before one can tackle a problem concerned with the mechanism of evolution.

In problem-based learning, the student is presented with an unknown problem. He or she must seek out the relevant information, formulate a hypothesis consistent with the observations, deduce predictions from the hypothesis, and subsequently accept, reject, or modify the hypothesis in accordance with the degree of fulfillment of the predictions. This model of learning has been variously defined as problem solving, critical thinking, reflective thinking, discovery, and inquiry. The mode of inquiry is the hypothetico-deductive style of reasoning that is the cornerstone of investigative science. Learning by this method has an important educational objective: the development of the habit of scientific thinking, characterized by objectivity, open-mindedness, skepticism, and the willingness to suspend judgment if there is insufficient evidence. It has been my experience that students, when given the opportunity, generate hypotheses quite naturally. Indeed, the practical problem is often one not so much of uncovering hypotheses as of holding them in check. As Charles Darwin once remarked, students have to learn to be wary of emotional commitments to their cherished hypotheses. Darwin wrote in his *Autobiography*: "I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it. Indeed, I have had no choice but to act in this manner . . ." (Vol. 1, pp. 103–104. F. Darwin (ed.). 1888. *The life and letters of Charles Darwin.* 3 vols. John Murray, London).

One of the most effectual ways of implementing problem-based learning is to organize the students in small discussion groups. The potential of learning groups in higher education has yet to be realized. One could argue effectively that group learning should be the principal, even the exclusive, process in a college course, and not a supplement to the usual lecture method. To ensure active participation by all members, learning groups are kept small—about 5 to 6 members. The student brings to the problem all of his or her previous educational experiences. The members of the group learn with and from each other, benefiting from their diverse backgrounds. The group develops a sense of responsibility for the learning progress of each member, and the students learn how to give accurate and candid feedback to each other. The process is often difficult because it represents a stark contrast to the previous competitive educational system to

which most students have been exposed. The tone of the group should be open and gentle; the attitude should be cooperative and mutually reinforcing. The personal interactions typically highlight strengths, weaknesses, and prejudices of the students, enlarging their view of themselves and enlarging their capacity to be open-minded, if not critical-minded.

Although the faculty member in charge of the small group is an expert or specialist in some branch of science, his or her role is primarily that of a generalist and a facilitator. The faculty member (often referred to as a tutor) must have the skills necessary to guide and facilitate discussion, as well as to design and assemble problem-based learning materials. The learning resources involve a variety of audio-visual techniques and educational approaches that include programmed learning. The tutor encourages and stimulates the discussion but does not direct or dominate the group. The initiative for learning remains in the hands of the students. The procedures are not open-ended, nor are the discussions free-wheeling. The group sessions are carefully planned, with explicit goals and activities.

The learning group is generally assigned one problem per week, and two or three sessions spread over the week are devoted to the problem. In evolutionary biology, each problem is designed to aid the student's understanding of a particular facet of evolution. As seen in *Appendix A*, one of the simplest, albeit instructive, problems involves the emergence and predominance in modern times of dark (or melanic) varieties of moths in the industrial areas of England and continental Europe. The problem is of particular interest because it represents a situation in nature in which an evolutionary change is not only observable but rapid as well. In the initial assessment of the problem at the first session, the students in the group identify the relevant components: smoke-polluted industrial regions, protective coloration, predatory birds (presumably insect-eating), and a host of other concerns. Once the dimensions of the problem are defined, the students discuss the observations and entertain a range of feasible hypotheses. If their knowledge is inadequate to immediately test certain hypotheses, the task becomes one of seeking out information in the library from textbooks and audio-visual presentations. Accordingly, the first session generally concludes with a discussion of the kinds of information that would appear to be necessary for the solution of the problem.

The second meeting of the group typically involves the application of the newly acquired data to the problem. The group members discuss how the new observations support some hypotheses and refute others. The group reviews all information and synthesizes a coherent explanation for the phenomenon being investigated. There inevitably arise questions of a general nature that warrant exploration and discussion. Examples of such questions might be: How do mutations arise? Is there a mathematical model for the process of directional selection? Can a deleterious recessive mutant gene be completely eradicated in a natural population by the severest form of selection? Extended discussions of such probing queries would provide for an instructive third group meeting during the week.

A more complicated problem, described in *Appendix B*, involves the emergence of multiple-resistant strains of bacteria to antibiotics. Several simultaneous mutations from sensitivity to resistance are usually hypothesized by students, but the emergence simultaneously of four or five different mutations to several different antibiotics must be viewed as highly improbable. The problem becomes particularly challenging as it involves facets of which most students are completely unaware, notably the phenomenon of the formation and exchange between bacteria of special episomes that carry several "resistance" loci. It has been observed that students learn best when researching a problem that is exceptionally challenging.

The development of intellectual skills beyond memorization and recall is generally a slow, frustrating process. Admittedly, progress in developing critical think-

ing skills is difficult to measure. Evaluation typically takes the form of written problems, in which the students are required to write out in detail their arguments for proposing one or more interpretations. The examination problems are of comparable difficulty to the problems explored in the group sessions. Several provocative essay-type questions are posed for a given problem. A sample examination problem appears in *Appendix C*.

For both student and teacher, the learning groups are stimulating and vigorous. It is my personal view that the basic philosophy and method are right, although a program of group learning is difficult to implement, particularly with massive numbers of entering students in large universities. I expect to be told that this remedy for science education is hopelessly impractical, but this does not deter me. Our present system of undergraduate education in the sciences is futile—it is too authoritarian, too inclined toward passive learning, too detached from the students' ongoing lives, and too impersonal. What is urgently needed is an educational program in which the students become interested in actively knowing, rather than passively believing. The students should be allowed to learn, not forced to learn.

When I first started teaching, I entertained the prospect that human conduct could be guided through knowledge and reason. If we could learn to make decisions based primarily, if not solely, on empirical evidence, we would be able to manage constructively our own destiny and construct a good, or better, society. In essence, through the habit of scientific thinking, we would develop rational insight. And, rational insight or intellectual self-awareness hopefully would reach a sufficient point to enable us to become free of irrational determinants.

Today I am less sanguine about eliminating the irrational determinants. I am now more interested in the skills of interpretation that the student possesses. I am content that the student develops the critical skills that enable him or her to distinguish between occult beliefs and objective knowledge. It may be too much to expect the average student to reject as false or invalid all ideas that are in conflict with empirical data. I do expect, however, that the students develop an attitude in which the concepts of science, particularly as they relate to evolution, are received in an open-minded manner, and given impartial consideration.

APPENDIX A

PROBLEM 1
INDUSTRIAL MELANISM

Slightly more than a century ago, dark-colored moths were exceptional in rural areas of England. The typical moth in the early 1800s had a light color pattern, which blended with the light coloration of tree trunks on which the moths alighted. But then the industrial revolution intervened to materially alter the character of the countryside. As soot and other industrial wastes poured over rural areas, the vegetation became increasingly coated and darkened by black smoke particles. In areas heavily contaminated with soot, the formerly abundant light-colored moths have been supplanted by the darker varieties. This dramatic change in the coloration of moths has been termed "industrial melanism." During the past two decades, several scientists, particularly E. B. Ford and H. B. D. Kettlewell at the University of Oxford, have analyzed the phenomenon of industrial melanism.

In the 1950s, the British Parliament passed the Clean Air Act, which decreed, among other things, that factories must switch from soft high-sulfur (sooty) coal to less smoky fuels. The enforcement of this enlightened smoke-abatement law has led to a marked reduction in the amount of soot in the atmosphere. In the 1970s, the University of Manchester biologist L. M. Cook and his colleagues reported a small, but significant, increase in the frequency of the light-colored peppered moth in the Manchester area.

Consider the issues. Provide plausible explanations for the phenomenon of industrial melanism.

APPENDIX B

PROBLEM 2
BACTERIAL RESISTANCE TO ANTIBIOTICS

In 1955, a Japanese woman who recently returned from Hong Kong developed a severe case of intestinal dysentery, which failed to respond to treatment with a variety of antibiotics. When the causative agent was isolated, it turned out to be a typical dysentery bacillus of the genus *Shigella*. This bacillus, however, happened to be very unusual. It proved to be resistant to four drugs, sulfanilamide and the antibiotics streptomycin, chloramphenicol and tetracycline. In the next few years the incidence of multiple drug-resistant dysentery in Japan increased. In fact, there have been a number of epidemics of intractable dysentery.

During a single outbreak of the disease on one occasion, resistant bacilli were isolated in some patients and sensitive bacilli of exactly the same type were isolated from other patients. Even the same patient may yield both sensitive and resistant shigallae. Moreover, the administration of a single drug (say, chloramphenicol) to patients harboring the sensitive organism may cause them to excrete bacteria that were resistant to all four drugs. It was then found that many of the patients who harbored drug-resistant shigellae also harbored strains of the relatively harmless colon bacillus *Escherichia coli*. The latter bacteria were also resistant to the four drugs.

Consider the issues. How can multiple resistance to drugs arise and be perpetuated in a given bacterial strain?

APPENDIX C

EXAMINATION 1
AUSTRALIAN RABBIT

The European wild rabbit has gained infamous notoriety in Australia as the most serious economic pest ever introduced on this isolated island continent. In 1858, a small colony of 24 wild rabbits was brought from Europe to the state of Victoria in the southeast corner of Australia. From such modest beginnings, the rabbits multiplied enormously and by 1928 had spread over the greater part of the Australian continent. Estimates placed the number of adult rabbits at over 500 million in an area of about 1 million square miles. In overrunning the open grassy plains, the rabbits caused extensive deterioration to sheep-grazing pastures and to wheat fields.

For many years the Australian government spent large sums of money on various measures to control the population explosion of these prolific rabbits. Trapping, rabbit-proof fencing, poisoning of water holes, and fumigation all proved to be largely ineffectual. Then, beginning in 1950, outstanding success in reducing the rabbit population was achieved by inoculating rabbits with a virus that causes the fatal disease *myxomatosis*. The deadly myxoma virus was implanted into the tissues of rabbits in the southern area of Australia. In a remarkably short period of time, the virus had made its way, aided by insect carriers, into most of the rabbit-infested areas of the continent. By 1953, more than 95 percent of the rabbit population in Australia had been annihilated.

However, after their drastic decline in the early 1950s, the rabbit populations begin to build up again. Moreover, the viruses in the rabbit hosts were found to be less virulent than they had been initially.

QUESTIONS

1. Provide an explanation for the emergence of less virulent strains of the myxoma virus in present-day rabbits of Australia.
2. Account for the fact that present-day rabbits in Australia show less severe manifestations of the formerly fatal myxomatosis.
3. Explain how evolutionary mechanisms play a role in the acquisition of host resistance to infectious disease.
4. Based on a variety of serological tests, the myxoma virus from North America differs appreciably in its infective properties from the myxoma virus of Australia. Predict the outcome of inoculating present-day rabbits of Australia with the North American strain of myxoma virus.
5. What has been the impact of repeated

past epidemics of tuberculosis and bubonic plague on the relative resistance of modern Europeans to these infectious diseases?

6. A virus depends entirely on the living host cell to provide the biochemical machinery and energy for its own replication. Explain how a virus takes over control of the protein-synthesizing capacities of the host cell and directs the apparatus toward synthesis of its own peculiar proteins.

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Science as a Way of Knowing—Evolution: The Biology of Whole Organisms[1]

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SYNOPSIS. Examples of current research of importance to the conceptual and informational bases of evolutionary biology in the areas of morphology, development, physiology, ecology, population biology, natural history, and systematics are discussed. A synthetic approach to problems that utilizes ideas and techniques from several areas of biology characterizes much current research, and it is providing new conceptual frameworks and new, testable hypotheses. Some of the possible problems with methods of presentation as we often teach in these areas of biology are considered.

The conceptual and informational bases of evolutionary biology continue to be strengthened through current research. Investigations of the biology of organisms, their relationships, and their interactions with the environment add to our understanding of pattern and process of evolution; indeed, science is a way of knowing.

The charge to suggest important current events in virtually all areas of organismal and supra-organismal biology that enhance our knowledge of evolution is a broad one, incredible in the literal sense of the word. At risk of having my sanity questioned, I accepted the charge when it occurred to me that each of us, when we design a course, faces that same task. Because of the breadth and diversity of morphology, development, physiology, behavior, ecology, population biology, systematics, and natural history, and in accord with constraints of space and time, I shall limit my comments to a few selected examples in these areas, especially emphasizing their contributions to new conceptual frameworks. I shall also note some other topics of current research interest, and comment on some of the problems with methods of presentation, as I perceive them. These comments are meant as suggestions, or possible guidelines.

I encourage you not to aggregate these examples in a "unit on evolution" within a course, but to use them to emphasize the concept of evolution as pervasive to our knowledge of biology. Biology is too often divided into "how it works" and "how it has come to work" halves, and it is most important that they be integrated, and focused on whole organisms. The examples I have selected can be treated in many different contexts, and in fact their unifying theme, along with evolution *per se*, is that each represents a synthesis of ideas and techniques from several areas of biology. This synthetic approach characterizes current research in all of the areas of biology that I have examined, and it is providing new conceptual frameworks and new, testable hypotheses. These ideas and examples can be presented at different levels of complexity and detail, so I shall risk giving too much information on some topics and too little on others for your various possible uses. These suggestions, which I hope provoke other ideas, can be amplified or generalized as appropriate to your courses and teaching styles.

MORPHOLOGY AND DEVELOPMENT

We often teach morphology, when we teach it at all in a first year course, in a highly typological way, selecting only a few examples. Morphology, I suspect, is most often presented in the context of animal and plant diversity, and I fear that students often come away from that exposure with a sense of the immutability of form, rather than of diversity and variation. Further, development is often presented, in both texts and lectures, as a study of regulation

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of processes that occur very early in the establishment of organisms, and development "stops" pedagogically with neurulation. Organogenesis and particularly the concept of ontogeny are not often dealt with, leaving students with little connection between "development" and "morphology."

However, recent work, much of it employing principles and techniques from both fields, has provided a new conceptual framework for understanding mechanisms and patterns of morphological change and diversification, constraints on size and shape, and the biomechanics of organisms. This emphasis is changing our understanding of the morphological changes that we see following speciation, as well as some aspects of the speciation process, and our assessment of the patterns of origins of major groups. Three examples illustrate this synthetic research.

In 1979, Alberch *et al.* presented a formalization showing how small changes in timing and rates during development might effect significant changes in morphology. In other words, quantitative changes in basic parameters of development can result in qualitative changes in morphology, and such perturbations are responsible for transitions among morphological body plans (Alberch, 1982). Alberch has argued that changes in body plan are constrained by the structure of postulated developmental programs, so he determined to test experimentally these ideas. Among both frogs and salamanders, there are numerous examples of species within lineages with different numbers of toes. Assuming that pentadactyly is primitive, the questions are: which toes are lost, in what sequence, and by what mechanism? Alberch and Gale (1983) devised a simple but elegant experiment to answer these questions. They treated limb buds on one side in a frog, *Xenopus laevis*, and a salamander, *Ambystoma mexicanum*, with the mitotic inhibitor colchicine and allowed development then to proceed. The treated limbs were smaller and had lost skeletal elements compared to the contralateral controls. Further, frogs always lost the first toe, salamanders the fifth. These differences then are correlated with qualitative differences in developmental sequence of digital differentiation in frogs vs. salamanders. Colchicine administration temporarily arrests mitotic divisions resulting in fewer cells and a smaller limb bud. This developmental retardation and reduced cell number result in a digital loss. Therefore, this is a continuous process (reduction of rate of cell division) with a strongly discontinuous outcome (loss of an entire digit, of many parts). It can then be inferred that a slight perturbation in developmental pattern could, assuming heritability and in concert with selection, effect a major morphological difference with long-range consequences. Slight differences in developmental programs and epigenetic regulatory mechanisms may be fundamental to morphological differentiation within lineages.

In addition to developmental and phylogenetic constraints on possible sizes and shapes, there are mechanical limits as well. The properties of the materials of which organisms are composed confer these limits, and design constraints are thus inherent. Trees are effectively towers that are open networks of cantilevered beams (stems and branches) that support many solar collectors (leaves) (Wilson and Archer, 1979). The problem is that trees grow, in contrast to engineers' towers. Beams get longer and thicker and produce new beams by branching. Beams (branches) are subject to bending and torsional stresses from the loads of self-weight, wind, etc. As the tree grows these forces increase, so the beams are stiffened to resist the forces against them. Different species have different leaf distributions and designs, and branching patterns, hence design is flexible enough to meet specific mechanical requirements. Strain stimuli affect rate of cell production, gravitational stimuli affect microfibril angle and internal strain; these are feedback systems. Wood rays in a tree limb are located so that they can sense strain in branches. McMahon (1975) demonstrates that these elastic criteria impose limits on biological proportions, and therefore metabolic rates in both plants and animals. Trees too tall and/or slender would be subject to buckling or compression. If branches are to

effect maximum lateral displacement from trunk so that leaves are exposed to light, there is also a point at which the length/weight ratio of a limb would cause bending toward the trunk. Elastic criteria in theory set length proportional to the $^2/_3$ power of diameter in both trunk and branches. Data on a diversity of species of trees indicate that the proportions of trees do not ever exceed this value, hence the theoretical prediction is supported. In animals shape also changes with scale. When a quadruped is standing, limbs are exposed to buckling loads and the vertebral column and its musculature to bending loads. When the animal runs, the situation is reversed, the limbs subject to bending loads and the vertebral column to buckling because of the thrust of limb propulsion. Again, length is proportional to the $^2/_3$ power of diameter. Surface area increases as the $^2/_3$ power of weight. This suggests that living organisms are required to adopt forms in which lengths increase, or scale, as the $^2/_3$ power of diameter. Somatic dimensions of a number of species of both plants and animals support this conclusion (McMahon, 1973). (There is nothing magic or universal about the 2/3 ratio; other significant biological relationships scale differently.)

Finally, Gans and Northcutt (1983) and Northcutt and Gans (1983) have utilized morphological and developmental data to propose a reinterpretation of the origin of vertebrates. They point out that most of the morphological and functional differences between vertebrates and other chordates occur in the head. Further, these structures are derived from epidermal placodes, neural crest, and muscularized hypomere. The derivatives of neural crest and epidermal placodes may have arisen from the epidermal nerve plexus of protochordates. Gans and Northcutt suggest that developmental changes are associated with a shift from filter feeding to predation, and more efficient patterns of locomotion and gas exchange led to reorganization of the pharynx, with elaboration of circulatory, digestive, and nervous systems and the development of special sense organs. Epidermal placodes and neural crest form special sense organs and other neural structures; developmental and endocrinological data support this idea (see below). It is now well known that neural crest contributes to connective, skeletal, and muscular tissue of the head. They hypothesize that electroreception developed as a means of detecting prey. Derived from epidermal placodes, electroreceptive organs were functionally enhanced by the deposition of hydroxyapatite. These deposits led to dentinous and enamel tissues to maintain the orientation of the sensory receptors, then to cartilage and bone, ossification therefore being a very late indicator of the vertebrate grade. Northcutt and Gans suggest that support tissues (cartilage, bone, dentine, enamel) arose in association with the new sensory organs, and only secondarily provided mechanical support. The development of dermal armor occurred later, and the orgin of axial vertebrae and a post-otic skull (composed of vertebral segmental elements?) is associated with the development of jaws.

This is an evolutionary scenario. It provides a new way of looking at the origin of vertebrates and at a number of questions of the origin of particular structures. It also provides a number of testable hypotheses regarding both development and function, in fact, more than the authors conservatively imply. For example, Gans and Northcutt suggest that monoclonal antibodies against neural crest or placodal tissue should be able to distinguish common derivation from these sources vs. independent ectodermal origin, and specific biochemical markers characteristic of neural crest should also occur in placode derivatives and in protochordate epidermal nerve plexus. Inducing perturbation in development might also be instructive, as neural crest transplant work suggests. One should not take pot-shots at parts of this scenario; one should test them.

PHYSIOLOGY

Evolution can be interwoven readily into the teaching of physiology, though physiological processes are often presented in a rather mechanistic way. It is important to associate physiological processes with whole organisms, and physiology with

responses of those organisms to their environment. Current research in several areas is providing important information for biologists. Work on aerobic *vs.* anaerobic metabolism in vertebrates and invertebrates (such as that of Bennett, 1982) is becoming important to our understanding of the evolution of major groups since it indicates that metabolic "efficiency" need not be associated with endothermy. Other kinds of studies of energetics are important to understanding evolution, and also involve multiple areas of biology, such as ecology and behavior. The physiological *costs* of reproduction, of feeding, of aggression, are significant variables for our assessment of life history evolution (see Congdon *et al.*, 1982). In fact, the work of physiological ecologists, focusing on responses of organisms, plant and animal, and the evolution of those responses, such as metal tolerance in plants, is an exciting and emergent area of study. Investigations into reproductive biology, including endocrine mechanisms, oogenesis and spermatogenesis, etc., are providing useful comparative data for understanding everything from reproductive timing to aspects of reproductive isolation. I draw on data from all of these areas, and morphology, development, and behavior, as I pursue studies on the evolution of live-bearing modes, including viviparity, in all vertebrates (Wake, 1982). A diversity of data is applicable to our analysis of plasticity, a concept now receiving considerable attention among evolutionary biologists. I shall focus on one particular example as a suggestion of the way that a physiological principle (mechanism) can be presented in an evolutionary context.

Dorothy Krieger elegantly summarized the evolution of brain peptides in a recent article in *Science* (Dec. 1983). The evolutionary origins of brain peptides and of polypeptide hormones are questions of great current interest because of several recent observations: 1) peptides considered to be of glandular origin have been found in vertebrate nervous tissue; 2) peptides thought to occur only in vertebrate glandular tissue have been identified in invertebrate neurons and in unicellular organisms; 3) peptide receptors have been found in unicellular organisms; 4) peptides previously known only in invertebrates have been found in vertebrate tissue; 5) and diverse peptides have similar sequences within and between species. Also, substances similar to hormonal peptides and neurotransmitters are present in plants and unicellular organisms. It is suggested that these peptides are primitive components of intercellular communication. Then in sponges, these messenger molecules are localized, and function as neurotransmitters. Coelenterates and annelids use peptides as both neurotransmitters and neurohormones, but lack endocrine tissue *per se*. Common brain-gut peptides occur in lampreys, and all other vertebrates. These observations suggest that so-called products of the nervous and endocrine systems were present before those systems evolved; as nervous and glandular tissues developed, the tissues expressed specific peptides previously diffuse in lower organisms. Common peptides occur in diverse tissues—hydra head activating factor, a coelenterate neuronal peptide, is present in vertebrate gastrointestinal tract and in neurons. ACTH and prolactin are present in vertebrate endocrine and neural tissue, and invertebrate neuronal tissue. Insulin occurs in vertebrate endocrine (pancreatic) tissue, but in both gastrointestinal secretory cells and neurons in invertebrates. It is also suggested that the neuronal system preceded the endocrine in an evolutionary time scale. Receptors also evolve, both in structure and in function. Prolactin in teleosts effects fluid homeostasis, but in mammals regulates secretion of mammary glands. Alpha-factor, a yeast mating pheromone, has extensive sequence homology with the vertebrate hypothalamic luteinizing hormone releasing hormone (LHRH), binds to rat pituitary LHRH receptors, and stimulates release of luteinizing hormone (LH) from cultured gonadotrophs. These observations suggest that the peptides are very old evolutionarily, and maintained throughout evolution. Further, a given peptide can act as a local factor, a hormone, a neurohormone, or a neurotransmitter in different instances, even within a

species (such as POMC, the ACTH precursor; a neurotransmitter in the brain, a hormone secreted by the pituitary, a neurohormone acting on gonadotroph function, and a paracrine factor in the reproductive and gastrointestinal tracts of certain vertebrates). In the course of evolution, then, the same peptide also may have changed function among these means of cellular communication. At any rate, this sort of research, and the synthetic view of it, give us a new framework for analyzing physiological processes, and similarity, variation, and change among organisms in an evolutionary context.

POPULATION BIOLOGY, ECOLOGY, AND NATURAL HISTORY

Work in these areas is highly complementary, often, as in areas of organismal biology, borrowing techniques and combining approaches to problems. For example, physiological ecology, already alluded to, is practiced by ecologists looking at resource use from energetic and evolutionary perspectives (Calow and Townsend, 1981). Behavioral ecology has become a synthesis of its own, as exemplified by Krebs and Davies (1978) (*Behavioral Ecology: An Evolutionary Approach*). Much of research in behavioral biology makes significant contributions to our knowledge of evolution. Analysis of such problems as coevolution—plant-animal interactions, parasite-host evolution—depends on both a conceptual framework and data drawn from application of diverse techniques. Conceptual advances have been made by introducing such ideas as game theory and the concept of the evolutionary stable strategy (Maynard Smith, 1982) and optimality theory (see discussions in Krebs and Davies, 1978; Oster and Wilson, 1978, and Alexander, 1982) in order to provide new frameworks for analysis in behavior, ecology, and life history "strategy."

I shall consider the analysis of sexual selection as one example of current research that is providing a new conceptual and informational base for evolutionary biology. Sexual selection is selection solely in regard to obtaining mates. Darwin envisioned the process of natural selection as giving rise to adaptations used in the struggle for existence. Later, as developed in *Descent of Man and Selection in Relation to Sex* (1871), he realized that natural selection cannot begin to explain many sexually dimorphic traits observed in nature because such traits would decrease the survival ability of the bearer; the traits are maladaptive in regard to natural selection. Therefore, he postulated the theory of sexual selection, explaining that traits which might even lead to decreased survivorship can still be selected for if they increase the ability of an animal to mate. The crucial distinction between natural selection and sexual selection, as drawn by Darwin, is that natural selection can result in the evolution of traits that increase survival ability, and sexual selection can lead to the evolution of traits that increase ability to attract mates even though they reduce survivorship. This distinction is lost when "Darwinian fitness" is defined as changes in allelic frequencies. So, Darwinian fitness is not what Darwin meant by fitness. Some have argued that the difference is semantic, since all we should be interested in is how allelic frequencies change; others have said that there is a crucial difference and the two should not be mentioned in the same breath. Regardless, the two forms of selection are processes and their modes of operation are different, and this needs to be understood.

Ryan (1983) has documented the costs and benefits of frog calls in terms of female choice of mates, effectiveness of communication, and male and female reproductive success. He and colleagues (Ryan *et al.*, 1982) also have documented the maladaptiveness of frog calls *vis-à-vis* natural selection. In *Physalaemus pustulosus*, a neotropical leptodactylid frog, the calls are a trait presumed to have evolved through sexual selection, and increase male reproductive success. However, the calls of the apparently most attractive males are also the most effective in attracting predators, thus decreasing the survival ability of the caller. In this case, sexual selection may actually oppose natural selection, and selection processes do not necessarily lead to maximization of population size, or other aspects of increase of "fitness." Another part of

research in sexual selection is that of the evolutionary consequences of female choice in the speciation process. The basic idea is that courtship signals of different populations of the same species diverge (adaptive or random divergence); this leads to reproductive isolation between populations since on re-contact potential mates either do not recognize each other or prefer mates from the local population. Then, as a result of a lack of gene flow between populations, the genomes begin to diverge and eventually there is a lack of genetic compatibility. These ideas are discussed by Arnold (1983) and West-Eberhard (1983).

The evolution of life history traits is receiving considerable attention, for it involves study of the natural history, population biology, ecology and physiology of organisms in order to understand the nature of and effects of such parameters as clutch size, reproductive period, age at first reproduction, life expectancy, and mortality. Tuomi (1982), Ballinger (1983), Berven and Gill (1983), Kaplan (1980) and Stearns (1980, 1983) have all provided recent new analyses of the evolution of life history phenomena, and that synthetic approach is important to our understanding of the nature of variation and its implications for evolution at the organism and population levels.

SYSTEMATICS

As I see it, the problem with systematics as it is dealt with in most courses is the presentation of a static taxonomy, into which organisms are pigeon-holed in order to have names, and a hierarchical arrangement of unquestioned relationships. In fact, systematics is a dynamic part of evolutionary biology, recently utilizing new techniques and new methods of analysis. One part of systematics is the description of recognizable, discrete entities, on the basis of distinguishing characteristics. Another is the ordering of species into a system of classification, based on shared characteristics. A third part is a phylogenetic interpretation of that classification. A major question today is the degree to which the classification hierarchy represents evolutionary events: order of descent from ancestors (the genealogy) and extent of divergence from ancestors, *i.e.*, evolutionary relationship and rate of change or divergence. Two themes pervade modern systematics—new methods of analysis of relationship, and the introduction of new techniques for assessing degree of relationship, or divergence from an ancestral stock. Systematists compare taxa, and then cluster them into groups using some similarity criterion. The three primary current methodological approaches to assigning rank, such as order or family, to units in classification hierarchies (Calow, 1983) are: 1) numerical taxonomy (phenetics, which assesses overall similarity, including both homology and convergence), 2) evolutionary or natural order systematics, which deals with genealogy and similarity and divergence with intuitive but not necessarily objective or universal rules for analysis, and 3) phylogenetic systematics (cladistics, or genealogical relationships based on shared derived characters, or homologies). Cladistics employs a rigorous methodology assessing shared derived characters to arrange related species in dichotomously branching sets. It assesses homology and polarity of characters. Pheneticists and natural order systematists first classify the taxa, then assess relationships. Cladists first reconstruct a phylogeny or genealogy of relationships of taxa, then design a classification consistent with the phylogeny (see Charig, 1982). There are strong adherents to each of these approaches. I will not go through their arguments, but it is important to let students know that systematics does not simply provide names and ranks, but it also provides an assessment of similarity regardless of descent, or an assessment of evolutionary divergence and relationship. There are different methods for illustrating these relationships. Cladograms, etc., "look different" from "Romerograms," and students will need to know why—both exist in textbooks, often without explanation. Students are forced to intuit what they mean, but these diagrams should be presented with an explanation of their bases.

Until recently classifications were based largely on morphological data. These were

assumed to be a fairly conservative expression of phenotypic variation, and homologies were used to assess similarity and divergence. Other kinds of characters (physiological, reproductive, life history, ecology, karyotypes) fairly recently have been incorporated into analyses. However, new advances in systematics are being made via the incorporation of techniques of biochemistry and molecular biology. These include electrophoresis of a diversity of proteins, microcomplement fixation, a quantitative immunological technique that counts the number of amino acid substitutions in a given protein in compared taxa, radio-immunoassay, and DNA-DNA hybridization. These methods allow comparisons among populations and species of the data generated. These are largely techniques for assessing *genetic* similarity. Most also give insight into modes of speciation and rates of evolution. An example of the utility of these approaches is provided by the work of Charles Sibley, a systematic ornithologist, who has evaluated the taxonomic relationships and evolution of birds based on morphology, behavior, electrophoresis and now DNA-DNA hybridization. He finds that the newer techniques provide phylogenies that often corroborate those based on morphology, but also may provide new evidence for different taxonomic associations based on genetic similarity (Sibley and Ahlquist, 1981, 1982). These techniques require new methods for analysis of these data as non-morphological characters that evolve, and numerous methods have been generated that can then be used by cladists, pheneticists, or evolutionary systematists. They also provide new data sets for evaluating competing evolutionary hypotheses, be they for evolution as a process in general, or specific to a group of organisms being assessed (see Mickevich and Metter, 1983).

In summary, we cannot present all aspects of both concept and information to our students. Time constraints, and those of materials and backgrounds, dictate this. Even so, I suggest that a minor "perturbation" or our "developmental" or teaching program is appropriate. We can then use principles of evolution to provide the conceptual basis for our teaching of *all* of the properties of organismal and supra-organismal biology throughout our courses, whether they are "general" or more specialized sub-fields of biology. This might allow students to integrate both concepts and their supporting data more efficiently than teaching a body of "facts" (which have a certain transmutability), thus reinforcing evolution as a major aspect of science as a way of knowing.

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I dedicate this paper to the memory of Ina H. Wake; member of the first BSCS writing team, teacher (and mother-in-law) extraordinaire.

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Science as a Way of Knowing—Molecular Evolution[1]

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SYNOPSIS. The teaching of evolution in introductory biology courses is critically discussed and those aspects of molecular evolution believed to be important for inclusion in these courses are briefly reviewed. Consideration is given to the use of biochemical and molecular biological procedures for studies of phylogenetic relationships and genetic variability, "classical molecular evolution and molecular population genetics," as well as the evolutionary basis of molecular biological phenomena, "neoclassical molecular evolution." The major results of classical molecular evolution and molecular population genetics studies are summarized and their implications discussed. Particular consideration is given to the neutralist—selectionist controversy and the processes accounting for differences in rates of organismal and molecular evolution. The scope of neoclassical molecular evolution is outlined and two subjects within this realm considered in some detail: i) experimental studies of the evolution of new genes and functions, and ii) the existence, maintenance and evolutionary roles of parasitic ("selfish") DNA and infectious inheritance.

INTRODUCTION

I have been assigned the task of considering the teaching of molecular evolution and the contributions of molecular biology to evolutionary theory. Thus, ". . . I have to be molecular. Who is not?" (A. Lwoff, 1966). While I shall fulfill my obligation to this charge, I have elected to interpret it rather broadly. I have also succumbed to the temptation of using this essay as a platform to display my biases about the teaching of evolution and the nature and scope of molecular evolution.

While this essay includes elementary reviews of specific areas of molecular evolution and molecular population genetics, it is not intended as a comprehensive review of the subject at large. I have concentrated on those areas, that for subjective as well as objective reasons, I believe should be included in introductory courses.

SOME OBSERVATIONS AND PREJUDICES

While evolution may well be the thread that ties all of biology together, concern about the fabric of the subject seems to have had little play in much of modern biology. There are professional biologists who would be indifferent to the title and substance of Theodosious Dobzhansky's 1973 essay "Nothing in Biology Makes Sense Except in the Light of Evolution." Indeed, as I found the other day, when speaking with a bright, and not-that-young, molecular geneticist, there are biologists out there who have never heard of Professor Dobzhansky. One can be a successful practitioner of many areas of contemporary biology without considering how organisms, molecules or phenomena came to be or their descent relationships. A relative absence of interest in evolution prevails in a number of areas of biology, with high-tech molecular biology being the most prominent of them. There are, of course, two possibilities: evolutionary theory and evolutionary considerations are of little utility in the study and understanding of many biological phenomena, or those of us who believe they are have failed to get our message across. I accept the latter.

It is my feeling that the limited interest in evolution and, in some cases, limited respect for its study as a scientific endeavor, is a reflection of how we teach it at the introductory level and beyond. The past 20 years have witnessed an extraordinary improvement in the quality and scope of introductory biology texts; a phenomenon that can itself be interpreted as a response to an intense selective pressure (Cox and May, 1982). Nevertheless, even in the apparent ancestor of this new wave of introductory texts, *Life* by G. G. Simpson,

[1] From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27–29 December 1983, at Philadelphia, Pennsylvania.

C. Pittenbrigh and I. H. Tiffany (1957), evolution is treated as a separate subject. Sometimes it is briefly considered in introductions and almost always relegated to final chapters for more comprehensive treatment. If evolution is the thread that ties it all together, and if without considering evolution nothing (or more realistically, little) in biology makes sense, evolutionary considerations should be present thoroughout texts and courses; a point also made by Dr. Moore and Dr. Wake in their essays.

To be sure, treating the evolutionary aspects and implications of all areas of biology covered would add material to the already excessive quantity introductory courses attempt to cover. However, many of these evolutionary considerations could be little more than vignettes, *e.g.*, the evolutionary reasons for anticipating a universal genetic code considered with the presentation of the code itself. By spreading the treatment of evolution throughout, it would be possible to cut down on its separate treatment. Under any condition, if the inclusion of evolutionary considerations throughout results in an increase in the ratio of concepts to facts,[2] then the intellectual yield of these introductory courses would necessarily be augmented.

In the main, the treatment of natural selection and evolution at the elementary level is extremely conservative. The history of a subject and some consideration of the personalities of its practitioners are useful pedagogical tools and, doubtless, increase student interest and appreciation for science as a human endeavor—I could not conceive of teaching Genetics from any but a historical perspective. On the other hand, the use of history and personality in the treatment of evolution at the introductory level sometimes borders on scholasticism, with Darwin playing the role of Aristotle. Do we really need tradition and authority to convince students of the importance and utility of evolution to the study of biology? Perhaps more than any other area of biology (I do not know for sure), evolutionary biology has maintained the school of thought advocacy tradition of earlier eras. Some hypotheses are more often championed than tested. Positions (almost always two for any given issue) are fiercely defended, even when they are not mutually exclusive. New ideas are liable to attack for no reasons other than their real, or even apparent, violation of orthodoxy. Could it be that our pedagogical preoccupation with tradition and personality has played a role in this?

The conservatism in the treatment of evolution at the introductory level is also reflected in the concentration on seemingly solved problems. As practicing scientists, much of what we talk about, think about and occasionally even work on are problems which are not solved. Much of the pleasure of being an evolutionary biologist is speculating on the answers to unanswered questions. Nevertheless, in teaching evolution at the introductory level, we tend to avoid giving the students the opportunity to participate in these speculations or, even worse, suppress speculation by presenting pat nonsolutions—to see what I mean, just consider the treatment of the evolution of sex in most introductory texts. While the display of humility in the face of unanswered questions may tarnish our facade of authority, the recognition of our limitations and the realization that they can make significant contributions to speculative discussions, will certainly increase student interest and self-confidence. Indeed, with their relative absence of preconception and bias, their contributions are likely to be even greater than ours.

As so clearly illustrated in Dr. Moore's essay, the study of evolution can be a scientific endeavor, even fulfilling the somewhat narrow "strong inference" criteria of Platt (1964). Nevertheless, in teaching evolution at the introductory level, the message that the study of this subject can be

[2] Perhaps, as minimal rule of pedagogical hygiene, we should not hold students responsible for memorizing facts that we have to relearn and rehearse before presenting. In their evolution, introductory texts have become increasingly encyclopedic. Thus, we can take comfort in knowledge that students have ready access to the facts, and can relax our efforts to cram these facts into their short-term memory.

scientific may well be garbled due to excessive noise. In our efforts to display the facts of evolution, we sometimes give too little consideration to the predictive elements of evolutionary theory and testable hypotheses generated from it. This is particularly true in introductory laboratories.

NATURAL SELECTION AND ITS LIMITATIONS

It is my feeling that the basic elements of natural selection should be presented very early in introductory courses. While the details of the genetic basis of natural selection require some understanding of transmission genetics, the process can be taught and well understood without formal genetics (Darwin certainly did well without it). I also believe that natural selection should be taught in a more general framework than it has been traditionally. While the statement may seem heretical, the pure Darwinian view of natural selection, which commonly prevails in our teaching of the subject at the introductory level, is unnecessarily restrictive. It is a universal process ("law"?), a property of transmitted (inherited) variation of replicating systems: molecules, cells, organisms, populations and communities. It will operate as long as the inherited variation is reflected as differences in rates of replication, be there a struggle for existence or not.

In addition to considering the process and potential of natural selection, we should also treat its limitations early in the course. It is not omnipotent and may well be quite myopic. As eloquently stated by King and Jukes (1969), "natural selection is the editor rather than the composer, of the genetic material. One thing an editor does *not* do is to remove changes which it does not perceive." It is also a process that is constrained by the evolutionary history of the population, the genetic basis of phenotype determination and conflicting selection pressures. Potentially fit variants may not be readily generated or may only be produced through a progression that includes variants that are less adapted than the parental forms. In cases where selection simultaneously operates at more than one level of replication, as it almost invariably will, phenotypes favored at one level, *e.g.*, the population, may be at a disadvantage at another, *e.g.*, the organism.

While the theory of natural selection can be taught and readily understood in a totally hypothetical framework, examples are of course useful. It is, however, critical that at least some of these examples provide direct evidence for the action of natural selection rather than being just *a posteriori* interpretations of phenomena, *i.e.*, "just so stories" (Gould and Lewontin, 1979). For students in introductory courses it would also be helpful to include examples with broad relevance. One example fulfilling these criteria is antibiotic resistance in natural populations of enteric bacteria. There is direct evidence for the existence of antibiotic resistant strains before human use of antibiotics and extensive documentation for the rapid increases in both the frequency of resistant strains and range of resistances borne by individual bacteria, following the clinical and prophylactic use of these substances (reviewed in Anderson, 1969; Falkow, 1975). The antibiotic resistance example also illustrates the various levels of replicating units and levels of action of natural selection. While some antibiotic resistance can be attributed to classical mutation-selection processes, most clinically important antibiotic resistance is coded for by genes borne on plasmids, *i.e.*, autonomously replicating genetic molecules. Furthermore, many of the actual genes responsible for the resistance are themselves parts of semiautonomous genetic molecules, transposons, which can be infectiously transmitted between plasmids and the host chromosome (Falkow, 1976; Cohen, 1976; Kleckner, 1978; Broda, 1979).

Introductory laboratories are not particularly amenable to high-tech molecular evolutionary investigations or long-term experimental studies. However, by using bacteria as a model system, some of the technical and temporal constraints precluding good experimental studies of evolutionary processes can be overcome. One of the most fundamental hypotheses of evolutionary theory, the preadaptivness (randomness) of mutations, can be directly

tested with the fluctuation test experiment (Luria and Delbruck, 1943). Within the course of a single laboratory, it is possible to demonstrate the basic elements of the classical theory of natural selection, exponential growth and the "struggle for existence." By extending these exercises to include a series of laboratory sections, in the course of a week, the process of adaptive evolution through mutation and selection could be demonstrated. I will gladly supply more details about these evolutionary exercises to interested readers.

With a more comprehensive view of natural selection and its limitations, selective neutrality, sexual selection, regressive evolution, parasitic ("selfish") DNA, transposition, and individually deleterious ("altruistic") characters are no longer special cases of evolution, but rather anticipated variations of a common principle. With a more pluralistic view of this process, we may even achieve some success in the campaign to purge the good-of-the species, progressive and Panglossian interpretations which continue to plague professional as well as popular considerations of evolution by natural selection.

CLASSICAL MOLECULAR EVOLUTION AND MOLECULAR POPULATION GENETICS

The majority of that which we currently consider to be Molecular Evolution and Molecular Population Genetics is in fact the application of biochemical and molecular biological technology to traditional evolutionary problems, determinations of phylogenetic relationships and the nature and magnitude of genetic variation in populations. While the evolution of molecules is observed in these studies, interest in molecules themselves and the molecular biological and biochemical implications of this evolution is secondary. For convenience and without pejorative implications, I shall refer to these endeavors as classical molecular evolution and molecular population genetics.

Some technological considerations

Since the turn of the century, immunological procedures have been used in taxonomic and systematic investigations (Nuttall, 1904). The well justified assumptions being that the phylogenetic relationships would be reflected in the extent of antigenic similarity of homologous proteins. The history of these serological studies of taxonomy and systematics is characterized by successive technological improvements increasing the precision of the quantitative estimates of phylogenetic distance. With the use of microcomplement fixation, these methods reached their peak of precision, in some cases being able to distinguish between proteins differing by single amino acids (Cocks and Wilson, 1969). At approximately the same time that the discerning powers of these immunological procedures were approaching their apex, amino acid sequence methods were being developed and comparative amino sequence data were becoming available for evolutionary studies. By the late 1960s, a large number of proteins from many different species were sequenced and catalogued (Dayhoff, 1972). For a review of these protein studies of molecular evolution see Wilson *et al.* (1977).

While the protein data provided quantitiative information about the degree of genetic identity of related species, to some extent the analysis of proteins was destined to be a transient period in the history of classical molecular evolution. Ultimately phylogenic relationships had to be based on DNA and, shortly after the appropriate quantitative procedures for DNA manipulation became available, they were applied to evolutionary studies. Initially, this was accomplished through quantitative determinations of the stability of inter- and intraspecific hybrid DNA molecules generated *in vitro* (Kohne, 1970). This was followed by the analysis of the fragments generated by treating defined blocks of DNA with restriction endonucleases (Kan and Dozy, 1978). With the development of procedures for identifying and isolating specific regions of DNA, cloning those DNAs with bacterial host-vector systems, and relatively facile methods for DNA sequencing (Maxam and Gilbert, 1977), it became possible to directly determine the degree of identity of homologous regions of DNA. While this, the seemingly ultimate technology for the molecular study of phylo-

genetic associations, has only recently begun to be applied for this purpose, central sources for the compilation and dissemination of these data are already in place and these data can be acquired on computer tapes from commercial sources.[3]

The development of the technology of Molecular Population Genetics was essentially parallel to that of that of molecular evolution. Serological data, inherited antigenic differences (primarily blood groups), were used for studies of variation within populations. Starting in the 1960s, protein electrophoresis began to be used for these types of investigations. This procedure provided relatively unbiased estimates of variation in structural genes that code for water soluble proteins (Harris, 1966; Lewontin and Hubby, 1966). It also permitted estimates of phylogenetic relationship between closely related taxa (Nei, 1971), which could not be accomplished readily with immunological and protein sequencing procedures. As was the case with empirical studies of molecular phylogeny, these protein based procedures were destined to be a tranisent phase.[4] Shortly after relatively facile procedures for the determination of quantitative differences in DNA became available, they were applied to studies of genetic variation. At first this was through the analysis of restriction enzyme fragments. Very recently, however, studies of within species variation in the DNA sequence of specific genes have been published (Kreitman, 1983; Milkman and Crawford, 1983).

Most of the molecular evolution and population genetic studies in eukaryotes have been concerned with chromosomal genes and chromosomal DNA. However, there have also been a number of studies of evolution and variation in mitochondrial DNA. In most cases these are accomplished through restriction fragment analysis (see reviews by Brown, 1983; and Avise and Lansman, 1983). DNA evolution in these maternally inherited extrachromosomal elements occurs at a relatively more rapid rate than that of chromosomal DNA and, as a result, mitochondrial DNA data permit relatively more precise estimates of genetic distance among closely related taxa (Ferris *et al.*, 1981).

The results and their implications

In many ways, the classical molecular evolution studies provide the single most compelling and readily presented evidence for the fact of evolution. Descent relationships are readily illustrated by comparing the amino acid sequences of the same protein in different species. For some proteins such as cytochrome c, these comparisons can be made for organisms in very distantly related groups, *e.g.*, yeast and humans. While proteins vary considerably in their rates of change, with only minor exceptions, the relative extent of sequence divergence among taxa remains constant and independent of the protein considered. At this juncture, I am unaware of any major differences in the phylogenies generated by adequately comprehensive studies employing both protein and DNA data. Nevertheless, it is clearly prudent to wait until a sufficient number of the returns are really in.

While the molecular evolution data added only additional support to the already overwhelming evidence for the fact of evolution, they had a profound effect on our view of the tempo and mode of the evolutionary process. Regressions between the number of nucleotide differences, estimated from the amino acid sequence data, and the divergence time of the organisms being compared, as determined from fossil evidence, are essentially linear; indicating that the rate of protein evolution was approximately constant in absolute (calendar) time. This observation suggested that the protein data can be used to estimate divergence time of extant organisms, *i.e.*, act as a "molecular clock" (Zuckerkandl and Pauling 1965; Fitch, 1976; Thorpe, 1982). Although in the great

[3] Bolt, Beranck, and Newman. Genebank Research Systems Division, Cambridge, Mass.

[4] While there may well be pressure to use the most up-to-date technology for many classical molecular evolution and molecular population genetic studies, older procedures are adequate and may well be more efficient.

majority of cases, the branching points of phylogenies generated with molecular data are consistant with those based on traditional, morphological criteria, for some groups there were very substantial differences in the apparent rates at which morphological and molecular evolution proceeded (Wilson *et al.*, 1977). Among the most dramatic of these differences in the rates of organismal and molecular evolution was that for the higher primates (for an interesting, and less technical account see Gribbon and Cherfas, 1982). Based on objective morphological criteria, humans and chimpanzees are placed in different families; if, however, these taxa were based solely on molecular data, humans and chimpanzees would be closely related members of the same genus (King and Wilson, 1975).

At the time that enzyme electrophoresis was first being used for population studies, there was considerable controversy about the magnitude of standing genetic variation maintained in natural populations. Morphological and serological procedures for studying genetic variation were necessarily biased; genes had to be polymorphic to be considered (however, see Lewontin, 1967). Although quantitative genetic (artificial selection) studies suggested that there was a substantial amount of standing genetic variation in natural populations of outbreeding organisms, the absolute extent of this variation was unknown. Protein electrophoresis represented the first method to allow for a relatively unbiased estimate of genetic variation. The results of these studies suggested that standing genetic variation could be quite substantial. On the average, outbreeding eukaryotic organisms are polymorphic (rare alleles with frequencies in excess of 5%) for approximately 30% of structural gene loci with the average degree of heterozygosity (genic diversity) being between 10% and 15% (see review by Nevo, 1978). The only prokaryotic species adequately studied in this manner, *E. coli*, has between four and five times as much genic diversity as outbreeding eukaryotes (Selander and Levin, 1980).

The neutralist-selectionist controversy

In many ways the results of these molecular studies ended an "academic"[5] period that population genetics was in at the time these procedures began to be used. The high rate of gene substitution, the relative constancy of this rate, and the substantial quantity of genic variation indicated by the molecular data came as surprises. These observations were not anticipated from the mathematical models of directional and stabilizing selection that were favored at the time or the prevailing interpretations of this formal population genetic theory. To some extent these deviations from theory were an artifact of the procedures used to calculate relative fitness. With different, but not necessarily more realistic, models, the observed frequencies of polymorphic loci could be accounted for by natural selection (Sved *et al.*, 1967; King, 1967; Milkman, 1967; Sved, 1968). On the other hand, these molecular data could also be accounted for by what is effectively a null hypothesis, *i.e.*, recurrent mutation and random genetic drift of *selectively neutral* alleles (Kimura, 1968; King and Jukes, 1969; Kimura and Ohta, 1971).

The recognition that the same body of molecular evolution and polymorphism data can be explained by diametrically opposing hypotheses, initiated the "neutralist-selectionist controversy," which has virtually dominated molecular population genetics for the past 15 years. The observed constancy of the rate of protein evolution could be accounted for by the neutral gene hypothesis, but was also consistant with the hypothesis of selection operating at a constant level, if averaged over long periods of time. Although the action of selection could be inferred for some protein polymorphisms, for most, the neutral gene null

[5] The word "academic" is used as in Stent (1969, 1978), as one of the phases in the history of a science: classical, romantic, dogmatic and academic. However, in Stent's view a science proceeds through this sequence only once. It is my impression that evolutionary biology cycles through this progression. Indeed, the same may be true for Molecular Biology, whose obituary Stent wrote in that 1969 essay.

hypothesis could not be rejected. While the neutral gene theory made very specific predictions about the number of alleles and distributions of allelic frequencies for polymorphic loci, the estimates of the parameters needed to test the fit of these distributions were difficult to come by and almost always equivocal. Thus, the controversy raged, techniques were improved, more data were gathered, additional models were developed, but an absolute resolution was not in the offing (for reviews see Lewontin, 1974; Nei, 1975, 1983; Clarke 1979; Nei, 1983; Kimura, 1983*a*, *b*).

It is my feeling that the neutralist-selectionist controversy is more a product of the sociology of science (the two camp-advocacy approach) than its substance. From a very superficial perspective, the neutral gene hypothesis appeared to be a challenge to Darwinian and neodarwinian orthodoxy. In point of fact, it is not and never was. Even its most staunch advocates, present it as a pluralistic hypothesis that accepts the constraints that natural selection imposes on genes and their products and sees natural selection as the unique force of adaptive evolution (see Kimura, 1983*a*, or more extensive, 1983*b*). It differs from naive selection theory only in the fact that it accepts the perceptive limitations of natural selection. Thus, even from the start, the neutral gene-selection question was a quantitative one of the relative contributions of random drift of selectively neutral alleles, and directional and stabilizing selection to molecular evolution and polymorphism. It remains to be seen whether future evidence will support the hypothesis that "the great majority of evolutionary changes at the molecular level are not caused by Darwinian selection but by the random fixation of selectively neutral or nearly neutral mutations" (Kimura, 1983*a*). I personally find the current evidence in support of this hypothesis to be very compelling.

Unequal rates of organismal and molecular evolution

To my mind, the most intriguing result of the molecular phylogeny studies was the observation that organismal and molecular evolution may proceed at different rates. This not only questioned the validity of divergence time estimates obtained from traditional, morphological procedures, but it also posed an additional challenge to the orthodox Darwinian and neodarwinian view of phyletic evolution as a smooth process operating through the gradual accumulation of allelic differences (Gould, 1980). These data also very clearly illustrated just how little is known about the genetic, molecular and developmental basis of morphological variation.

Could it be that changes in structural genes of the sorts being considered in classical molecular evolution studies are *not* those primarily responsible for major morphological differences in closely related organisms? It seems almost certain that the answer to this question is yes. To be sure, it is possible that small modifications in the activities (but not the functions) of enzymes, or in the structures of nonenzymatic proteins, that may result from single nucleotide substitutions, may yield major morphological modifications. However, changes in the genes regulating the time of action and/or level of product formation of these structural genes seem far more reasonable as candidates for the genetic basis of major phenotypic differences (Wilson, 1976; Wilson *et al.*, 1977).

At this time, eukaryotic developmental biology is not yet at a stage where a direct test of this *regulatory gene hypothesis* is possible. However, there is clear evidence for genes with regulatory functions in eukaryotes. One fine example of this is the bithorax complex of 12 or more loci which play a role in the development of the major body segments of *Drosophila melanogaster*. Flies homozygous for mutant alleles at two loci in this complex have four wings, rather than the one pair of wings-one pair of halteres as is the case for wild-type *Drosophila* (Lewis, 1963; and review by Hunkapillar *et al.*, 1982). There is also circumstantial evidence in support of the hypothesis that regulatory gene changes play a major role in the determination of species differences. The concentrations of homologous pro-

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teins in the same tissues of different species can differ by a factor of ten or more (Wilson *et al.*, 1977). The results of experimental studies with bacteria also provide evidence for the potentially dominant role of regulatory gene changes in adaptive evolution. When wild-type, lac inducible *E. coli* are grown in lactose limited chemostats, constitutive mutants rapidly evolve (Horiuchi *et al.*, 1962). While these regulatory gene changes may be supplemented by increasing the number of copies of genes in the lac region, to increase β-galactosidase concentration, Horiuchi and his colleagues failed to find any evidence for changes in the structural gene coding for this enzyme. The studies of the evolution of new metabolic functions in bacteria, described in the following section, provide additional evidence for the importance of regulatory mutations in adaptive evolution.

NEOCLASSICAL MOLECULAR EVOLUTION

Early in the classical period of molecular evolution and molecular population genetics it was reasonable, or at least convenient, to give only secondary consideration to the molecular biological and biochemical processes being studied. However, within short order, it was apparent that a deeper consideration of these processes was required for interpreting the results of these evolutionary studies. Part of this more ecumenical perspective came as a direct byproduct of the neutralist-selectionist fray. It was clear that more had to be known about the constraints natural selection posed on the products of structural genes. This stimulated more detailed studies of the physiological, biochemical and ecological basis of selection of polymorphic enzymes of known function (see review by Koehn *et al.*, 1983, and the studies by Dykhuizen and Hartl, 1980). As a consequence of exposure to the technology of molecular biology, evolutionary biologists, were seduced into considering the evolutionary basis of some of its phenomenology, see for example the transposon studies of Biel and Hartl (1983) and Chao *et al.* (1983). In addition, and largely independently of the work proceeding in classical molecular evolution and molecular population genetics, biochemists and molecular biologists were studying or speculating on the evolutionary aspects of biochemical and molecular biological phenomena. Included among these endeavors were theoretical considerations of: i) the evolution of the genetic code (Jukes, 1983); ii) the evolution of accessory elements in bacteria (Campbell, 1981, 1983); and iii) the origin and evolutionary role of exons and the phenomenon of split genes (reviewed in Hunkapillar *et al.*, 1982). Also included in this category are various studies of the molecular basis of the origin of life. For convenience, I shall refer to investigations, where primary consideration is the evolutionary basis of molecuar biological phenomena, as neoclassical molecular evolution.[6]

The scope of neoclassical molecular evolution is substantially broader than that of classical. Thus, even in this superficial review, it is necessary to limit my consideration of it. The neoclassical evolutionary problems considered below were chosen because: i) I find them to be particuarly interesting; ii) I believe that they should be considered in introductory courses; and iii) they are not now given adequate (or, in most cases, any) treatment in introductory texts.

The evolution of new genes and phenotypes

For the most part, the mechanisms by which new genes and new phenotypes evolve have been restricted to speculation supplemented by primarily *a posteriori* interpretations of evolutionary processes (see for example Horowitz, 1965; or Jensen, 1976). There have, however, been a number of elegant experimental studies of gene evolution using bacteria. The results of these are intriguing in their own right, have important implications for some observations of classical molecular evolution, and illustrate the potential for exper-

[6] In the Stent (1969, 1978) interpretation, the classical period would be followed by a romantic. Maybe so!

imental studies of molecular evolutionary processes.

These studies of gene evolution in bacteria have been primarily concerned with the acquisition of new metabolic functions. Most commonly, they take the form of experimental sequences intiated by challenging populations of bacteria with substances that they are incapable of metabolizing, "novel" substrates, as unique resources and letting mutation (sometimes at augmented rates) and selection play out their roles. Occasionally, but certainly not invariably, mutants capable of growth on the novel substrate are isolated. In most cases, the capacity for growth on the new substrate by the initial mutant is modest and open to improvement. The experimental sequence then proceeds with additional rounds of mutation and selection to augment the rate of growth on the novel resource. These "Directed Evolution" studies have been reviewed by Clarke, (1978); Mortlock (1982); and Hall (1983).

In these experimental studies, new functions are acquired and improved on by both regulatory and structural gene modifications. This is illustrated in the pioneering investigations of this type by E. C. Lin and his colleagues on Xylitol utilization in a strain of *Klebsilla aerogenes*. The parental strain used in this experimental sequence could take up Xylitol by diffusion, but could not grow on it. The first mutant capable of growth on Xylitol acquired this capacity through the constitutive production of the hydrolytic enzyme necessary for the fermentation of Ribitol, ribitoldehydrogenase, RDH. While RDH normally was capable of oxidizing Xylitol as part of the D-arabitol pathway, Xylitol does not induce the D-arabitol operon. By starting the second cycle of mutation and selection with these first order xyl+ mutants, Lin and his colleagues were able to obtain Xylitol fermenting mutants with 2.5 fold higher growth rates on Xylitol than the parental mutant. These second order mutants were the result of a mutation at the RDH structural gene which increased the activity of RDH enzyme on the Xylitol, but not on the Ribitol substrate. Mutations leading to further increases in growth rate on Xylitol were generated from these second order xyl+ strains. In this case, the phenotype change was acquired by regulatory mutation at the D-arabitol operon leading to the constitutive production of the D-arabitol permease, which was also capable of transporting Xylitol.

While the details of the scenarios by which the capacities to utilize novel substrates are acquired vary among species and substrate, the combined role of regulatory and structural gene changes are essentially typical. This also seems to be the case when the substrate is not novel to the organism, but where the structural gene required for fermentation is deleted. One example of this is lactose metabolism in *E. coli* via the ebg operon. Mutants of this type were first isolated by Campbell *et al.* (1973) and the evolution at the ebg operon has been extensively studied by B. Hall and his colleagues. In this situation, the original strain was deleted for the lacZ (β-galactosidase) locus and the acquisition of lactose fermenting phenotype required mutations at two loci, i) a structural gene, ebgA, that was responsible for the synthesis of the hydrolytic enzyme EBG (for evolved β-galactosidase), and ii) a regulatory mutation, ebgR that was necessary to increase the level of EBG synthesis. The ebgA and ebgR loci are two of three genes in an operon that is genetically very distant from that of the classical Lac operon (66 min as opposed to 7 min the *E. coli* K-12 chromosome) and the EBG hydrolytic enzyme has no apparent homology with the lacZ β-galactosidase.

By further rounds of mutation, recombination and selection, additional ebgA and ebgR alleles were selected using a variety of different β-galactosides as challenging substrates. In this manner, Hall and his colleagues obtained mutants of regulatory as well as structural genes with products that varied in their substrate affinities. One of the selected ebgA mutants was capable of converting lactose into a substrate capable of inducing the classical Lac operon, something the original ebgA could not do, but classical lacZ β-galactosidase could.

I see two major messages to be learned

from these studies of directed evolution in bacteria. First, they suggest that regulatory genes play a major role in the process leading to the evolutionary modification of structural genes. Second, they suggest that the affinities of enzymatic and regulatory proteins can be quite malleable. By changes in the concentrations of these enzymes or by modest changes in their structure, such as those acquired by single nucleotide substitutions, the role of these structual gene products can be dramatically changed.

Molecular perversities: Parasitic DNA and infectious inheritance

Until very recently, most evolutionary theory was restricted to chromosomal, stay-at-home, genes that are transmitted vertically between generations. This is, indeed, a restrictive view of the genome and the evolutionary process. The bacteria abound with autonomously replicating DNA molecules, plasmids and phage, as well as a variety of semiautonomous DNAs, insertion sequences, transposons and vestigial prophage. Through either their own devices or by hitchiking, these autonomous and semiautonomous genetic molecules can be infectiously transmitted between cells. While some of these "accessory" genetic elements may not determine specific host-manifest phenotypes, it is clear that as a class they play a significant role in the adaptation and evolution of bacteria. Some do code for potentially adaptive host phenotypes (antibiotic resistance is only one of many extrachromosomally determined characters) and conjugative plasmids and phage serve as vehicles for the infectious transfer of chromosomal DNA (Falkow, 1975; Reanny, 1976; Campbell, 1980).

The significance of autonomous and semiautonomous DNA and infectious inheritance in the adaptation and evolution of eukaryotes is just beginning to be evaluated. It is clear that analogous genetic elements are present in eukaryotic cells and that multicelled higher organisms have substantially more DNA than they appear to need. Some evidence and compelling arguments suggest that much of this accessory DNA is nonfunctional, essentially parasitic ("selfish"), and is present as an artifact of evolution at the subcellular level (Doolittle and Sapienza, 1980; and Orgel and Crick, 1980).[7]

Although the phenomena of parasitic DNA and infectious inheritance have yet to work their way into the classical evolutionary literature, it is my feeling that some consideration of them should be included in introductory biology courses. These DNAs serve as examples of molecular evolution at the subcellular level and, in spite of their selfish nature, they and their capacity for infectious (horizontal) transmission may play an important role in organismal evolution.

Natural selection and the maintenance of parasitic genetic molecules

It seems reasonable to assume that as a consequence of various kinds of replication errors, renegade copies of DNA (as well as RNA) will be continuously generated. While some of these additions to the genome may be selected for at the organism level, *e.g.*, by gene amplification, others may not be under positive host selection. However, if the rate of replication of these analogs of selfish DNA exceeds their rate of loss, they can become established and will be maintained in that organism. There are essentially two non-exclusive mechanisms by which this "overreplication" (Campbell, 1981) can obtain: i) by coding for some phenotype which enhances the fitness of their host; or ii) by infectious transmission. If the former mechanisms are involved in the maintenance of these DNAs, then from the perspective of their host cell, they are not "selfish." While innocuous (selectively neutral) parasitic DNA may persist for extended periods of time, as long as there is some finite rate of loss, they would require continuous de novo production for their persistence.

[7] While generally not presented in that light, all DNA not coding for phenotypes that are under direct selection at the level of the organism or the population, fulfill this parasitic-selfish criteria. This includes the DNA produced by various kinds of duplication processes as well as the "pseudogenes" that most likely arise by relaxation of selection pressures (Ohno, 1970; Li, 1983).

Natural selection would, of course, favor mechanisms for overreplication in parasitic genetic molecules. This was recognized by Doolittle and Sapienza (1980) and Orgel and Crick (1980) and was fundamental to their "selfish DNA" intepretation (also see Dawkins, 1982). On the other hand, the fact that overreplication would be favored is not a sufficient condition for the maintenance of these elements. Natural selection in this situation is necessarily a multilateral process involving the immediate host cell, the whole organism (if multicellular) and, to a lesser extent, the population. In cases where the cell is the whole organism, as it is for bacteria, this coevolutionary process is a seemingly simple matter and, on *a priori* grounds, there are conditions where these elements can be maintained solely by infectious transfer (reviewed in Campbell, 1981 and Levin and Lenski, 1983). There have not been many formal considerations of the conditions for the maintenance of selfish genetic molecules in eukaryotes. It is, however, conceivable that some become established and are maintained by distorting segregation ratios in their favor (Hickey, 1982), or by infectious transmission as viruses. It is also possible that these elements are sufficiently innocuous to become established in populations solely by recurrent de novo synthesis in a manner analogous to that of selectively neutral alleles (Kimura, 1968). In the latter case, they would accumulate at a rate equal to their rate of production.

Selfish DNA, infectious inheritance and adaptive evolution

From the perspective of organismal evolution, parasitic DNA may have absolutely no role. It could be no more than artifact of natural selection operating at the molecular level and the constraints and myopia of natural selection operating at higher levels. Thus, as suggested by Doolittle and Sapainza (1980) and Orgel and Crick (1980), quests to ascertain the phenotype of these DNAs could be in vain. On the other hand, the fact that these DNAs do not determine specific host phenotypes does not necessarily imply that they have no role in the adaptive evolution of their hosts. Parasitic DNA is the raw material of genome expansion and, in this light, adaptive evolution operating through genome expansion is a byproduct of the subcellular evolutionary processes leading to the establishment and maintenance of parasitic DNA (also see Cavalier-Smith, 1978, 1980). There are compelling arguments and some evidence that transposible parasitic DNAs play a role in hybrid dysgenesis and thus may be important in the speciation process (see reviews by Rose and Doolittle, 1983*a*, *b*). Rose and Doolittle (1983*a*) have also suggested that selection for horizontal transmission by parasitic DNAs could have resulted in the evolution of sex in eukaryotes (perhaps, the major unsolved evolutionary problem). This, is almost certainly the case for plasmid and phage mediated gene transfer in bacteria, where chromosomal gene recombination (sex) is an accident of the infectious transmission of these elements (Levin and Lenski, 1983).

One of the most impressive aspects of biological evolution is the production of the extraordinary amount of diversity and complexity of organisms in the relatively short span of time available. Even accepting the possibility that the processes leading to punctuated branching in phylogenies also augments the rate of evolution, it seems worth questioning whether the diversity and complexity of organisms has been generated solely through evolution along species lines. It is clear that the rate of evolution would be accelerated if vertical genetic transmission was supplemented by horizontal (infectious) gene transfer between lineages. In this way, phenotypes that evolve in one lineage could be precipitiously acquired by members of other lineages. In the bacteria, it is clear that this process does operate (Reanney, 1976). In one or more steps, plasmids and phage can be transferred between genetically very different hosts. In the course of their travels, they can pick up transposons and chromosomal genes from one host and transmit them to another. With appropriate selection pressures, these acquired genes may become incorporated in the recipient genome.

At this time, we know relatively little

about the role of infectious inheritance in the evolution of extant higher eukaryotes. While this process may be important for unicelluar eukaryotes, on the face of it, it seems unlikely that it plays a very significant role in the adaptation and evolution of multicellular eukaryotes. Although there are viruses that could conceivably serve as vectors for gene transfer, if pathological viruses are typical of viruses in general, the host range of these vectors would be limited. Furthermore, even if gene transfers did occur, for these genes to become incorporated into the host genome, they would have to work their way from the infected somatic cells to the gametic genomes. While there would clearly be selection pressures for autonomous and semiautonomous DNAs to work their way from somatic cell lines to gametic, for the reasons considered earlier, the mere existence of these selection pressures is not sufficient. On the other hand, there is no evidence to suggest that viral mediated interspecific gene transfer does not occur and that the moved DNAs can not become incorporated into the recipient genome. I personally would not be at all surprised, if the results of DNA sequence studies provide evidence for a significant role of infectious inheritance in evolution and adaptation of multicelled eukaryotes.

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Films, Filmstrips and Videotapes in Evolutionary Biology[1]

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As a member of a college or university faculty, each of us is aware of the value and importance of using audiovisual resources in classroom and laboratory instruction of the biological sciences. Films, filmstrips and videotapes, when carefully and skillfully integrated into the teaching process, provide innumerable benefits to the student. They can, for example, clarify and simplify difficult biological concepts, provide an intellectual framework in which to understand and evaluate critical issues created by current advances in biology, and present a stunning blend of scientific facts and photography that makes learning a lively and rewarding experience. And, as Dr. Moore has made clear in his elegant essay, students should be made aware that science is a human endeavor, done by human beings to answer questions of human interest. Films and videotapes can dramatize this point quite convincingly. In short, audiovisual resources can capture the excitement of the biological world and thereby spark student interest and learning.

The various speakers of this ASZ Education Committee sponsored symposium have clearly developed the rationale and importance of the proper teaching of evolution in college- and university-level biology. The teaching of evolutionary biology, using the suggested strategy of integrating articulated concepts with the evidential basis for them, is easily augmented with a wide variety of exceptionally high quality films, filmstrips and videotapes. These may be purchased, rented, or made available on a short-term loan basis. However, as I learned in putting together the Film Program portion of this symposium, identifying subject material appropriate for classroom or laboratory use in evolutionary biology and then locating the appropriate films or videotapes are not always easy tasks. A beginning step in the selection of audiovisual material is to consult with your college or university Audiovisual or Media Resources Center (or, if unavailable, the reference staff of the library). Many major colleges and universities have media centers with a wealth of information, principally in the form of catalog listings, pamphlets, etc., on circulating collections of films, filmstrips and videotapes. Additionally, these same centers frequently offer a wide range of services to facilitate your use of film and video resources, including reference staff prepared to answer questions on film or videotape content, selection and utilization.

The selection of films, filmstrips or videotapes in evolutionary biology can be made by perusing titles and descriptions in subject area catalogs, and/or by computer search of an online data base. With either approach, the title of a film or videorecording is usually accompanied by information on release date, running time, format (black and white or color), and location or distributor. In addition to the listings in publications available from college or university Media Resources centers, the following catalogs may be of benefit to you: *National Geographic Film and Video Catalog* (National Geographic Society, Educational Services, Dept. 83, Washington, D.C. 20036); *Time-Life Video—16 mm Film and Video Catalog* (Time-Life Video, 1230 Avenue of the Americas, New York, N.Y. 10020); and *The Educational Film Locator of the Consortium of University Film Centers* (R. R. Bowker Co., 1180 Avenue of the Americas, New York, N.Y. 10036). The availability of computers and advances in information technology now make it possible and convenient to make systematic searches for appropriate audiovisual materials. The

[1] From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1983, at Philadelphia, Pennsylvania.

data bases of the following three networks may be of use to you: AVLINE (data base of the National Library of Medicine), OCLC (Ohio College Library Center) and RLIN (Research Libraries Information Network). One or more of these data bases are available through most academic libraries.

Listed below are the titles of 16 mm films that might be helpful to you in the teaching of evolution and natural selection. Many are also available in videocassette. Keep in mind that the list is by no means complete.

The Ascent of Man: 1—Lower Than the Angels
The Ascent of Man: 9—Ladder of Creation
The Ascent of Man: 13—The Long Childhood
The Asteroid and the Dinosaur
The Botanic Man: 2—The Crucible of Life
The Botanic Man: 3—Living Water
The Botanic Man: 4—Potential Energy
The Botanic Man: 7—White Death, New Life
The Botanic Man: 9—Extinction is Forever
Charles Darwin (marvelous impersonation by Dr. Richard Eakin from Great Scientists Speak Again Series)
Did Darwin Get It Wrong
Dr. Leakey and the Dawn of Man
Evolution (a delightful and fanciful animation of evolution produced by the National Film Board of Canada)
Evolution and the Origin of Life
Five Billion Years
Fossils: Clues to the Past
From Homo Erectus to Neandertha!
Galapagos Cactus and Scalesia
Galapagos Finches
Galapagos Tortoise
Hot-Blooded Dinosaurs
The Incredible Shrew
Introduction: The Experimental Conditions
Islands Within Islands Within Islands
Leakey
The Legacy of L. S. B. Leakey
Life on Earth (27 individual programs; videocassette rental only)
Lucy in Disguise
Marine Iguana
Mendel: Father of Genetics
Message in the Rocks
Molecular Evolution
Monkeys, Apes and Man
Mystery of Animal Behavior
Natural Selection: Evolution at Work
Pelicaniform Birds of the Galapagos
Protective Coloration
Restless Earth: Evidence from Ancient Life
Sea Lions and Fur Seals
Search for Fossil Man
Species and Evolution
Strategy for Survival: Behavioral Ecology of the Monarch Butterfly
The Dinosaur Hunters
The Tool Users
This Was the Beginning
Part I—The Invertebrates
Part II—The Vertebrates
Tobias on the Evolution of Man
Variations on a Theme: Skeletal Adaptations

Reviews of new films and videotapes in evolutionary biology may be found in *Biological Abstracts/RRM, Library Journal* (R. R. Bowker Co.) or *Science Books and Films* (AAAS). Facilities are usually available at media centers with circulating collections for prospective users who wish to preview a film or videorecording. Distributors will often provide preview copies or preprints of new titles if purchase is being considered.

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Science as a Way of Knowing—Evolutionary Biology[1]

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SYNOPSIS. This essay is part of an educational project of the American Society of Zoologists that will make proposals for improving the first-year biology course in the universities. The detailed suggestions emphasize the importance of the conceptual framework of the biological sciences. The topic for this year is Evolutionary Biology and it is developed largely by the hypothetico-deductive method emphasizing that science, in addition to its store of information, is a way of knowing. Other topics will be considered in future years in the ongoing project.

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[1] From the Symposium on *Science As a Way of Knowing* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1983, at Philadelphia, Pennsylvania.

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WHY A NEW EDUCATIONAL PROJECT?

The problem

The state of education in the United States is widely regarded as a national crisis that severely compromises the present and future. However, members of the American Society of Zoologists, together with other biologists, are in a position to deal with some of the problems of education in a significant manner.

This optimism is based on the fact that the ASZ members, together with other biologists, occupy responsible posts in the major institutions of higher education and, therefore can exert great influence. University faculties set the curriculum for what is taught in the universities and play a major role in educating those who will teach in the schools. This, in turn, determines what is taught as biology in the pre-college years. This central role of the universities places a special obligation upon them. Whereas a generation ago it was thought that educational reform should start at the high school level, it is now widely recognized that it should begin at the university level. So long as our universities train the teachers, any reform in the pre-college courses must be preceded by the reform of the teaching in our universities. (This argument is greatly expanded in Moore, 1981.)

Inadequate biological education is especially serious, since biology is the science most frequently elected at all levels. For many students a biology course will not only introduce them to the world of life but will also be their total experience with the world of science.

One measure of our failure in teaching may be seen in the present conflict between biologists and creationists. Ignorance and misunderstanding of the evolutionary process, and what is science and what is not, would not be so pervasive if we had discharged our professional responsibilities more effectively in recent decades.

The members of the ASZ Education Committee wish to identify the reasons why education in science fails to meet societal requirements and to begin remedial actions. In this endeavor, we seek cooperation of the full membership of the American Society of Zoologists and of our sister societies. Seven of them have already indicated their interest in and support for this project by cosponsoring this first effort. This is a task for all biologists. A few ASZ committee members can do little, but with the involvement of biologists as a whole, we can do a very great deal.

The possible cause

Our preliminary analysis suggests that a major portion of the crisis in science education results from our overemphasizing facts, especially those relating to the exciting discoveries in modern biology, without providing a conceptual framework for the science. We convey more information than understanding. You can test this assumption for yourself by asking your students what is the evidential basis for some of the important concepts in biology. Can your students tell you *why* we think that genes are parts of chromosomes; why we think that the substance of heredity is (nearly always) DNA. Why, in spite of the tremendous variation in structure and function, we recognize a class of objects as "cells"? Why do we assume, beyond a reasonable doubt, that organisms evolve? See if you can find *any* important concept that your students can support with adequate data and argument.

A decade ago Paul Doty and Dorothy Zinberg (1972) had some forceful observations to make on our problems. This is what they had to say:

> The greatest overall threat to a science education that aims to remain viable and useful for a long time is that it will succumb to the temptation of being current. With a great burst of scientific discovery having taken place in the quarter century just behind us, with half of the scientific literature having been written in the last dozen years, with half of the Ph.D.'s granted in the United States awarded in the last nine years, the urge to be current, to be modern, is unavoidable. In proper measure, it is essential for orientation and motivation of the student and for the establishment of the bench marks by which future develop-

ment is measured. In excess, the student drowns in a world of facts and concepts for which he is unable to recognize the precedents and from which he is unable to project the future.

So, how do we solve the dilemma of orienting and motivating the student without drowning him? It may be simpler to reach an accomodation that will be acceptable to the student than to the professor of biology. After all, it is the teacher, not the student, who is aware of all those facts and exciting discoveries. For a student who is still at the stage of being unsure whether or not blood is the physical basis of inheritance, the details of the chemical structure of the genetic materials may not be as exciting, or as meaningful, as the professor might suppose.

Many of our best teachers agree that the essence of education should be to provide students with the conceptual framework of a field. Facts come and go—not necessarily because they are wrong, but because they become uninteresting or irrelevant. A conceptual framework, however, gives meaning to existing data and allows one to integrate new data and thoughts into a meaningful whole. The conceptual framework of a field is constantly adjusted and remodelled but it is never discarded. Once learned, it is not easily forgotten.

It might have been predicted, for example, that the conceptual framework of the field of biological classification would have undergone a revolution once Darwinism became accepted. Darwinism provided an explanatory hypothesis for the resemblances and the differences among organisms—and that is what classification is all about. The new view saw variation among organisms as a reflection of evolutionary processes yet the conceptual framework of systematics remained. Darwinism enriched the conceptual framework but it neither destroyed nor even greatly modified the then existing scheme of classification.

Plans for the Science as a Way of Knowing *project*

Innovation in education is much like innovation in evolution in one important respect: we can neither predict the success of a new program nor of a new species. Recognizing this, the ASZ Education Committee proposes to begin some experiments—offer suggestions for making the first-year college and university courses in biology more effective. Each year, for as long as this project is useful, we will organize symposia for the Annual Meetings and produce written materials that will offer suggestions for how the major areas of biology might be included in a first-year university course. The sequence might be something like this:

1983. Science as a Way of Knowing—Evolutionary Biology
1984. Science as a Way of Knowing—Genetics
1985. Science as a Way of Knowing—Developmental Biology
1986. Science as a Way of Knowing—Biology and Human Affairs
1987. Science as a Way of Knowing—Cell Biology
1988. Science as a Way of Knowing—Physiology
1989. Science as a Way of Knowing—Animal Kingdom
1990. Science as a Way of Knowing—Ecology

All of this is tentative. The information that we obtain from this first year's experiment will be the basis of future plans. Once the cycle of topics has been completed, it will start over. By that time not only will the fields have changed but so will many of those responsible for the first-year courses. The cycle is long and it might be useful to think of scheduling two topics for a single year. Coverage of rapidly developing fields could be made more frequently than more slowly developing fields. Somewhere in this schedule there must be consideration of the overall organization of the course—how much emphasis can be allowed for each topic. If our project proves useful, hopefully we can elicit the cooperation of botanists. We are after all talking about biology, not just zoology.

The plans for each year will be much the same until experience shows us how to do

things better. There will be two symposia. A General Symposium will involve two or three speakers, each offering a personal suggestion for how the topic for the year might be developed. A Special Symposium will identify those aspects of current research that are so noteworthy that they should be included in a first-year course—and hence will eliminate something else. The dual approach of these two types of symposia may help us to balance what is timeless with what is timely.

The organizer of each year's symposia will prepare a written essay presenting his point of view. This will be distributed at the sessions. The document you are now reading is the essay for the first year.

It goes without saying, but we intend to emphasize it none the less, that we do not accept that there is a single approach to excellence in education. We will offer no single model and each symposium speaker will present what seems to him to be worthy of consideration. All we are asking is that you think about what is proposed and take for your own what you feel is useful and important. Surely there is much fine teaching in first-year university biology courses, yet collectively what we do cannot be accepted as satisfactory since the results do not always meet the requirements of the students or of society. We must seek new and better ways of educating our students in the science of biology.

First, I will ask you to consider some of the rules that one should observe in teaching any part of biology: pedagogical themes, if you will. Following this, the bulk of the essay will be devoted to suggestions for teaching evolutionary biology, the topic for 1983.

The suggested approach: science as a way of knowing

The title of our project summarizes in six words our philosophy of teaching science. This philosophy will be presented briefly now in a series of suggestions and then put into practice in the specific proposals for teaching evolution.

No matter what major area of biology is being considered, we suggest that the following principles should be followed.

First, it should be made abundantly clear to the student *what the problem or question is.* Science is a way of seeking answers to questions about natural phenomena and it will be far easier for the student to understand the answers if he is aware that there is a question. This suggestion may seem too obvious to be mentioned but recall some of the lectures you may have heard recently. Did you always know why the research had been done? Was it clear what problem was being illuminated by the data presented?

Second, *try using the hypothetico-deductive approach in presenting topics* to your students. This approach is not very different from the "common sense" procedures we use in solving everyday problems—a point worth emphasizing to your students. The hypothetico-deductive procedures are among the most important methods that enable us to know things in science. They can be powerful adjuncts to teaching as well.

Scientific knowledge begins with a question—not surprising since there cannot be answers unless there are questions. Some phenomenon of nature is observed, we become curious about it and wish more information. It is nearly impossible to obtain an answer to any important question in science unless we first make a guess about what the answer might be. This guess is our *hypothesis.* The guessing is not a random affair. The guess will be based on various observations, hunches, and clues. This process, in which we combine the specific bits of information and logic to produce a more general statement (a hypothesis) is known as *induction.*

There is an absolute requirement for the hypothesis: *it must be testable.* Thomas Hunt Morgan explains it this way:

> It is the prerogative of science, in contrast with the speculative procedures of philosophy and metaphyscs, to cherish those [hypotheses] that can be given an experimental verification and to disregard the rest, not because they are wrong, but because they are useless.

It is well to emphasize to students that, surprising as it may seem, the most difficult part of scientific procedures is to know what

questions to ask and then be able to formulate useful hypotheses and deductions. F. S. C. Northrop (1947) has this to say:

> There are many reasons for believing that perhaps more than anywhere else it is at the beginning of any investigation that the source of genius is to be found. For what characterizes a genius like Galileo, Lavoisier or Einstein is the economy of thought and effort by means of which he achieves his result. Each one of these men found the key factor in the situation and went directly to the heart of the problem which had been baffling to his predecessors. The methods which all three used at later stages in their investigations are well known. It was in finding the key difficulty and in knowing precisely at what points to direct the well-known methods that the genius consists.

The point that Northrop is making is that genius consists of knowing not only what questions to ask but how to seek an answer.

So we have our question and we have formulated one or more hypotheses that represent possible answers. We continue by saying, if the hypothesis is true, the following consequences must follow. These consequences are *deductions.* If the hypothesis is true, as we are assuming, the deductions must also be true. Then we set about *testing the deductions* by making observations or performing experiments. If the data from the observations or experiments show that the deductions are incorrect, then we must either abandon the hypothesis or modify it to conform to what we observed from the tests. If the deduction proves to be true, then we can say that the hypothesis *may* be true—at least it has not been falsified so far. The more deductions that are tested and found to be true, the more likely it is that the hypothesis is true. Should we be able to formulate and test critical and elegant deductions and they continue to be verified, we reach the stage when we can say that *the hypothesis is true beyond reasonable doubt.* The hypothesis then becomes a statement that is part of the conceptual framework of the field.

In summary, then, the idealized view of scientific methods and the method being proposed to teach science are:

1. Ask a question.
2. Develop an hypothesis by induction.
3. Make deductions from the hypothesis.
4. Test the deductions.
5. Use conclusions from the tests to validate or falsify the hypothesis.

Third, *whatever data are obtained must share this essential characteristic: they must be obtainable by other scientists.* That is, the data must be verifiable. If an important discovery is made, it is never fully accepted by the scientific community until it has been verified by other scientists. If the original discoverer has made an error, the error would likely be corrected when others attempt to verify the original report. *Science tends to be a self-correcting way of knowing.*

These three suggestions: making the question or problem explicit, using the hypothetico-deductive mode in teaching, and emphasizing that science is a self-correcting enterprise, should provide students with understanding as well as information. Here are some additional suggestions that you may wish to consider. They have to do with the specific strategies of teaching.

Teaching strategies

A. Do not introduce data unless they are to be used to answer some question or illuminate some concept. The amount of data that can be presented to students is, for all practical purposes, unlimited. Therefore, selections have to be made. All information has some value but that value increases greatly if the information becomes part of some conceptual construct. Beware of facts for facts' sake. Charles Darwin would have approved of this suggestion. In a letter to his friend, Henry Fawcett, he wrote, "How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service" (F. Darwin, 1903, vol. 1, p. 195).

B. Do not make the mistake of assuming that, just because something has been known for a long time, it is not worthy of presenting to your students. Many of the basic concepts of biology, especially of evo-

lutionary biology, are quite old. They are still basic and they will not be old to the student who does not know them. More often that not, the questions asked and tentatively answered by biologists long ago are the sorts of questions that will puzzle a student first approaching a field of knowledge. In addition, there are frequently resemblances between a logical analysis of a problem that we might make today and the actual historical steps of discovery.

C. From time to time emphasize that science is a human endeavor—done by human beings to answer questions of human interest or human importance. This may come as an astonishing revelation to your students. Science is closely related to human concerns—intellectual, medical, technological, social, or economic. Science is done by human beings who have the normal range of strengths and limitations of human beings in general. When scientists get up in the morning, the males at least, put their pants on one leg at a time.

D. Although my main emphasis so far has been on the conceptual basis of science, we must always remember that science bases its statements on data. It is as pointless to teach concepts without giving the evidential basis for them as it is to teach facts without giving the conceptual framework that they subtend.

So much for suggestions about teaching science in general. Now follow some suggestions for teaching evolution in the first-year university course.

TEACHING EVOLUTIONARY BIOLOGY

The first suggestion is to treat it seriously and allow sufficient time for its presentation. There is a real gap between what biologists say they want to do and what they do when it comes to teaching evolution. On 28 November 1958, the famous geneticist H. J. Muller addressed the Central Association of Science and Mathematics Teachers, meeting in Indianapolis. His title was "One Hundred Years Without Darwinism are Enough." Muller was concerned that evolution was taught either ineffectually or not at all in the schools. But let him tell it (Muller, 1959):

> It ill befits our great people, four generations after Darwin and Wallace published their epochal discovery of evolution by natural selection, to turn our backs on it, to pretend that it is unimportant or uncertain, to adopt euphemistic expressions to hide and soften its impact, to teach it only as one alternative theory, to leave it for advanced courses where the multitudes cannot encounter it, or, if it is dealt with at all in a school or high school biology course, to present it as unobtrusively and near the end of the course as possible, so that the student will fail to appreciate how every other feature and principle found in living things is in reality an outgrowth of its universal operation.
>
> Are we teachers in whose hands lies the responsibility of bringing to the next generation a true and modern view of the nature of things, as gained by the devoted efforts of the world community of critical scientific minds, not deeply ashamed that we have been so remiss in our task of awakening in that developing generation an adequate realization of the most basic forces of life and of how these forces have worked and are still working to give rise to all life's outer manifestations? Why dabble around with the superficialities of our subject and bemuse our young charges with technical terms and baffling complexities if we do not make fully clear to them the deepest known meanings and unifying underlying principles and if we do not show from step to step, in a true perspective, the ways in which these principles have engendered all the other manifold features of living things?

Muller was talking mainly about the biology of the pre-university years where the fundamentalist religions were a powerful force in preventing the teaching of evolution in the schools. But, as Muller wrote,

> we have no more right to starve the masses of our people intellectually and emotionally because of the objections of the uninformed than we have a right to allow people to keep their children from

> being vaccinated, and thus endanger the whole community physically.

Muller saw the intellectual starvation of our masses as terribly dangerous.

In an equally well known essay, "Nothing in Biology Makes Sense Except in the Light of Evolution," Theodosius Dobzhansky (1973*a*) summarized his position after surveying the major fields of the biological sciences:

> Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts—some of them interesting or curious but making no meaningful picture as a whole.

These essays of Muller and Dobzhansky made considerable impressions but seemingly little impact on what is actually done in the classroooms. I do not know of a single biologist who does not regard evolution as the basic concept of the biological sciences. This is true to such a degree that it has become an almost unacknowledged point of view. It *is* the way we think. But our students do not come to us thinking that way.

And therein lies the problem. All too often the professional biologist takes evolution for granted and assumes that his students need not be instructed. This becomes obvious when the sequence of topics for the introductory courses is planned. Quite frequently, evolution is relegated to the very end. The reason usually given is that evolution will have much more meaning if all other topics in biology are treated first: evolution is said to make sense only when there is a firm basis of biological knowledge. But if we really believe, along with Muller and Dobzhansky, that evolution illuminates all the rest, we cannot relegate it to the end of the course.

A possible compromise could be to consider evolution, at different levels of detail, in several places in a course. One might start, for example, with a brief introduction to evolutionary biology near the beginning of the course. A single lecture, or possibly two, could introduce students to the fundamental notion that the organisms of today are the descendants of very different sorts of organisms that lived in the past. The mechanisms of evolutionary change—natural selection and other ways—would have to be postponed until genetics has been treated.

If this suggestion is followed, it would then be possible to use the concept of evolutionary change to illuminate many of the biological phenomena considered in the course. These phenomena would "make sense" when it was realized that they had a history and what they are today is a consequence of that long history.

One of the more poignant aspects of our brouhaha with the creationists is our insistence that evolution is the unifying theme of the biological sciences while at the same time we use it so uncertainly in our general courses in university biology. Is it really our unifying theme?

Defining some terms

When discussing evolution it is especially important that we indicate to our students how we intend to use terms such as "theory," "hypothesis," "proven," "fact," and "concept." My usage follows.

Theory for a scientist may represent the grandest synthesis of a large and important body of information about some related group of natural phenomena. For non-scientists the term may be pejorative: "evolution is just a theory," meaning that it is a dubious notion. Both of these very different meanings, together with others, are fully countenanced by lexicographers, so it is essential that students know how the term is being used.

I will use "theory" as a term applying to a body of knowledge and explanatory concepts that seek to increase our understanding of ("explain") a major phenomenon of nature. Thus, the Cell Theory would be taken to consist of the many sorts of observations—morphological and physiological—relating to the basic units of structure and function of most living creatures.

Used this way, a theory cannot be disproven. There is no way that the Cell Theory can be falsified. Some of the things we think we know about cells may be shown

to be false but the consequence of this will be that some of the data or concepts included in the Cell Theory will be eliminated or replaced by other data and concepts that are more probable. Theories are never disproved, only improved.

Theories are so important and so nearly coextensive with the fields of knowledge for which they provide the conceptual framework that, quite frequently, the term "theory" is abandoned. Thus, the books appearing today are not entitled "The Cell Theory." More likely the title will be something such as "Cells" or "The Biology of Cells."

One can acknowledge the usefulness of a theory even though the ultimate causes of the phenomena to which it applies are unknown. Thus, one can accept the Theory of Gravitation as a useful synthesis of available knowledge relating to the mutual attraction of bodies—and yet have no adequate understanding of what "pulls" them together.

Hypothesis for me is a tentative explanation of some phenomenon. It is an "educated guess." Many use "theory" and "hypothesis" as synonyms. I will not. In the formative years of a science, hypotheses may grow into theories. Some of the early speculators about the underlying causes of organic diversity and of adaptation adopted an hypothesis of evolutionary change to account for these phenomena. As data and certainty increased, one could begin to recognize a large body of information and verified hypotheses as the "Theory of Evolution."

I will use *concept* to mean the intellectual framework of a theory or a generalized way of looking at a phenomenon. I usually prefer to speak of the "concept of evolution" rather than "theory of evolution" just so the listener will not think I am talking about some dubious hypothesis.

A scientific statement is "true" if all attempts to falsify it have failed. So used, the term means "true beyond all reasonable doubt." In general, I think we overdo this tentativeness of scientific statements. Good form, I know, but it can be carried to foolish extremes. Cannot we accept as "true" that water is composed of hydrogen and oxygen? Then again, some statements are true because they are definitions. An experienced ornithologist, after having a good look at a medium size bird with a grayish back and a reddish breast, does not have to be so precious as to say that the bird is "a robin beyond all reasonable doubt." We have agreed that a bird with certain well-defined features is to be known as a "robin." If the experienced ornithologist has seen a bird with those features it is, by definition, a robin.

We can also accept that historical events that have left adequate records need not be verified by experiment or by observation of a rerun of the event. One can accept the reality ("truth") that dinosaurs once existed without making them evolve through the many steps from primitive amphibians through primitive reptiles to their magnificent selves. There are many things in biology that cannot be repeated experimentally or verified by direct observation. This does not mean that we exclude them from the domain of science—a fact that the philosopher Popper (1976) seemed not to have understood (see Williams, 1973).

For a biological phenomenon to be *proven* means to me that it has been tested extensively and elegantly and has not been falsified. Once again this means, especially for important phenomena, "proven beyond all reasonable doubt."

What are the questions?

The hypothesis of evolutionary change smoldered in the human intellect from the days of the early Greeks. It came into full flame during the 19th century when interest in natural history was intensified. Travelers, scientists, and professional collectors brought back to Western Europe a bewildering variety of new kinds of animals and plants from all parts of the world and even from the depths of the ocean.

As familiarity with living organisms increased, so did questions about them. The sorts of questions that eventually led to the concept of evolutionary change were varied but the main ones seem to have been these three.

1. How could one account for the

extraordinary amount of organic diversity? What was the explanation for all those species, hundreds of thousands and possibly millions of them, and with their amazing differences in structure, behavior, and way of life?

2. How could one explain the remarkable adaptations of living creatures? The more one learned about the structure and behavior of organisms, the more remarkable was their exquisite adjustment to the life they led. The intricate structure of a bird's feather, as revealed by the microscope, showed it to be a contrivance perfected for lightness and strength. Bones are generally thick and heavy but some of the bird's bones are hollow and the walls thin. The lungs of birds extend into air sacs, which both lightens the body and improves respiration. The entire bird seems to be a perfect solution to the problem of flight. No human engineer could duplicate the bird's remarkable achievement. All of man's attempts to fly had ended in death or ridicule.

3. What was the basis of the *scala naturae*, or scale of nature, that saw all species of animals or plants as part of a continuum that, with small gaps, appeared to extend from the simplest to the most complex species? One could start with some fish, such as sharks, and find a sequence of types extending through the dolphins to the great whales. One could pass in small steps from typical lizards, through lizards with ever-shorter legs, to snakes with no legs at all. There seemed to be patterns in organic variety.

How does one seek answers?

It is not obvious. Even with our knowledge today of what the answers proved to be, can we imagine any direct research program that might be expected to provide answers to the three questions just listed? What can your students suggest? What would we want to observe or subject to experiment? Some of your students may see the difficulty: not one of our three questions has been formulated in a manner precise enough to enable us to use the procedures of science to seek an answer. One cannot begin to make observations or conduct experiments with a question. One must start with a provisional answer—a testable hypothesis—if there is to be any hope of gaining some understanding of the phenomenon. In science, we might almost say that we seek answers to "answers." We cannot just ask why there is incredible variety in the world of life. We have to make a guess—hypothesis—for what the reason might be and then set about seeing if it is so.

The traditional answer: Divine Creation

We will start by briefly considering how people attempted to answer our three questions about two centuries ago. One available answer, the age-old notion of evolution, had been revived by several writers—Lamarck (1809) and Chambers (1844). Neither made a convincing argument. The main reason for this was that science and society already had an explanation for adaptation, the diversity of organisms, and related matters. This explanation, itself thousands of years old, was well established in Western thought. It was Divine Creation, as described in Genesis. God had created everything, animals, plants, the earth, and the cosmos at some remote time in the past—some said as long ago as 4004 B.C. The many sorts of animals and plants of today were each a consequence of an act of Divine Creation. The remarkable adaptations were an example of the care exercised by the Creator. That the species could be arranged in an almost continuous scale of variation meant only that they were created that way. Whatever one observed in nature was the consequence of the specific events of creation. There were no real problems. Every question relating to cause had the same answer—that is the way God did it.

One might have supposed that the belief that what organisms were and did depended directly on Divine Creation would have stopped all serious study. Far from it. It was reasoned that one might learn about the Creator from studying what He had created. This approach, which was known as *Natural Theology*, had its beginnings in England with the Rev. John Ray (1627–1705; see Raven, 1950). Ray's philosophy

is given by the title of his most famous book (1691): *The Wisdom of God Manifested in the Works of the Creation.* The title, he explains, means "the Works of God at first, and by him conserv'd to this Day in the Same State and Condition in which they were first made." No change; no evolution.

And Ray could accept no other explanation than Divine Creation:

> every Pile of Grass or Ear of Corn sufficiently proves [that God exists] for, they say all the Men of the World cannot make such a Thing as one of these; and if they cannot do it, who can or did make it but God? To tell them that it made itself, or sprung up by Chance, would be as ridiculous as to tell the greatest Philosopher so.

In answer to our question why there are so many species, Ray wrote that an example of God's "infinite Power and Wisdom [is] the vast Multitude of Creatures, and those not only small, but immensely great [which] are Effects and Proofs of his Almighty Power."

Our question about adaptation has the same explanation. "The admirable Contrivance of all and each of them, the adapting all the Parts of Animals to their several Uses, the Provision that is made for their Sustenance" is all the work of the Creator.

An example of "adapting the Parts of the same Animal one to Another . . . is the proportioning the Length of the Neck to that of the Legs." That is, if animals are to have legs upon which to stand, they must have a neck of appropriate length, otherwise they "could not conveniently gather their Food or Drink if they wanted a Neck." All species that need a neck of appropriate length have one except the elephant. The problem for the elephant is that its head is so massive and heavy that it could not be suported by a neck of sufficient length to allow the head to reach the ground. The solution was to create an elephant with a trunk on the front of its head to enable it to secure food and water.

Natural Theology continued to flourish and remained the most conceptually developed part of biology almost to the time of Darwin. Darwin and Huxley were thoroughly familiar with a widely read book of William Paley (1743–1805), Archdeacon of Carlisle, *Natural Theology; or, Evidences of the Existence and Attributes of the Deity, collected from the appearances of nature* (1802). Most of Paley's appearances were collected not from nature but from John Ray, without giving credit. In any event it is a well written summary of Natural Theology.

Natural Theology reached a remarkable peak with the publication of the *Bridgewater Treatises* between 1833 and 1836. The Right Honourable and Reverend Francis Henry, Earl of Bridgewater, left a sum of 8,000 pounds sterling to be invested and the interest used to have a series of books written:

> On the Power, Wisdom, and Goodness of God, as manifested in the Creation; illustrating such work by all reasonable arguments, as for instance the variety and formation of God's creatures in the animal, vegetable, and mineral kingdoms; the effect of digestion, and thereby of conversion; the construction of the hand of man, and an infinite variety of other arguments; as also by discoveries ancient and modern, in arts, sciences, and the whole extent of literature.

In all there were eight treatises covering subjects in biology, geology, mineralogy, meteorology, chemistry, physics, and astronomy. They provide a synthesis of science for the early years of the 19th century. Those in biology were especially successful in covering the field. They included many observations of the sort that Charles Darwin was to use in support of his hypothesis of evolution by natural selection. In fact, one cannot read the *Bridgewater Treatises* devoted to biology without being struck by how slight a change in emphasis would be required to switch from the hypothesis of Divine Creation of species to an hypothesis of creation of species by evolution. So far as obtaining the data are concerned, Darwin need not have made that Voyage of the Beagle—he could have stayed home and obtained enough facts for his theory from the *Bridgewater Treatises.*

Within three decades after publication of the *Bridgewater Treatises,* the Divine Cre-

ation hypothesis began to be replaced in the minds of most scientists by the hypothesis of evolution. Kuhn (1970) employs the term "paradigm" to mean a generally accepted way of explaining a scientific phenomenon of first magnitude. Divine Creation was one paradigm for explaining the phenomenon of organic variation, adaptation, the scala naturae, and much more. The paradigm of evolution was a different way of explaining the same phenomena. Kuhn observes that one paradigm may replace another in what he calls a "scientific revolution." A scientific revolution will occur when the old paradigm ceases to be a useful and acceptable way of explaining the phenomena to which it applies. Your students may find Kuhn's analysis of interest. His scientific revolution represents one way of knowing being replaced by another way of knowing.

Some useful references to the topics considered so far are Mayr (1982), J. C. Greene (1959), Gillispie (1951), Eiseley (1958), Glass (1959), Wells (1963), Hooykass (1972), McPherson (1972), Adams (1938), Osborn (1894), Knight (1972), and Geikie (1905).

The Darwinian answer: evolution

In the autumn of 1859 one of the most influential books of all times was published: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* The author was Charles Robert Darwin (1809–1882), an English gentleman naturalist whose writings on coral reefs, geology of South America, barnacles, and a voyage of the exploring ship *Beagle* had been well received.

Darwin was interested in answering the three sorts of questions that have been our concern. He was rather successful in doing so but, of greater importance, he started lines of investigation and thought that have continued to be highly productive to this day. He succeeded where others had failed because of his insistence that only naturalistic data and concepts be employed. All before him had invoked to some extent supernatural explanations, mainly—what we find today is a consequence of Divine Creation. The 19th century scientists were becoming increasingly reluctant to accept supernatural explanations. For some the fact that supernatural forces could explain anything and everything meant that they could explain nothing. In all fields science was advancing rapidly and what had seemed impervious to analysis a generation before was succumbing to careful observation and experiment.

One of the great advantages of having Charles Darwin introduce the modern version of the subject of evolution to students is that he explicitly uses the procedures that scientists are supposed to use—mainly the hypothetico-deductive method. He tells us what made him consider the hypothesis of evolution at a time when it was held in low esteem. Then he tells us what he did: "The line of argument often pursued throughout my theory is to establish a point as a probability by deduction and to apply it as hypotheses to other points to see whether it will solve them" (quoted by Ghiselin, 1969, p. 4).

Antecedents to the hypothesis of evolution by natural selection. The stage of induction

First, what observations suggested that the hypothesis of evolution might be worth considering? What were the clues that suggested to Darwin that some explanation other than Divine Creation might be possible? This putting of clues and observations together to form a hypothesis is known as *induction.* Induction is a logical step from specific statements to more general statements, in contrast with deduction where one begins with a general statement (the hypothesis) and moves to the more specific deductions. There were three clues, according to Darwin, all dating from the years he spent on H. M. S. Beagle and becoming clearer after he had returned to England and discussed them with other naturalists. These three observations are casually referred to in the first sentence of the Introduction to the *Origin* and in more detail in his *Autobiography* (see Barlow, 1958, p. 118; also see Sulloway, 1982*a* and 1982*b* for a different interpretation).

1. While the Beagle was engaged in

charting the coasts of Argentina, Darwin conducted considerable field work on land, stimulated in part by his susceptibility to *mal de mer*. He observed many species that were new to him. Some were very strange, such as the armadillo. Darwin was also collecting fossils and among these he found the remains of some extinct armadillos—the glyptodonts. The clue is this: two very strange animals of the same general sort, one living and one extinct, were observed in the same part of the world.

What hypotheses can your students give for this observation?

2. Darwin visited many localities on the east coast of South America from Brazil to southern Argentina. He noted that some of the species that he encountered in one locality might be present at other places yet the individuals in the various localities might not be exactly the same. Thus, the clue is that what appeared to be the same species was made up of local populations that varied with the locality. Individuals from populations close to one another might differ almost imperceptibly, while populations more distantly separated might be almost as different as two species. This phenomenon is known as *geographic variation*. It was not the sort of thing Darwin had observed in England. There all of the individuals of a species were very much alike. But England is small and the climate does not vary greatly from place to place.

Can your students suggest a hypothesis for this observation?

3. A similar phenomenon was encountered in the Galapagos, a group of volcanic islands off the coast of Ecuador. One of the most striking kinds of animals there are the giant tortoises. It was pointed out to Darwin by one of the residents that each island had its own variety of tortoise. The differences were such that an experienced person could tell the island from which any individual originated. Here was geographic variation occurring on islands within sight of one another. He noted similar examples in some species of plants and birds. The Galapagos finches remain to this day a notable example (Lack, 1947).

Had you been with Darwin, would this last observation have suggested evolution to you, especially in view of the almost universal rejection of that hypothesis by authorities in biology and geology?

Formulating the hypothesis of evolution

Darwin convinced himself that the three observations just listed could be explained on the basis of evolutionary change. The standard explanation in the 1830s would have been that both the extinct armadillo-like creature and the living species had been separately created. If so, Darwin asked, isn't it surprising that both the fossil form and the living form are found in precisely the same part of the earth? The living animals were scampering over the land that held the entombed fossils. Wouldn't it be simpler to assume that the extinct form evolved into the living form?

With respect to the phenomenon of geographic variation, Darwin wondered just how precise Divine Creation had to be. John Ray had said that living species are exactly the same as the day they were created. That would seem to mean that each local population of a species, no matter how slightly it differed from the neighboring populations, represents a distinct act of Creation. Did a slightly different sort of tortoise have to be created for each little island in the Galapagos?

On the other hand the phenomenon of geographic variation could be explained on the basis of evolution. The hypothesis would go something like this. A widespread species on the South American mainland would find its local populations in a variety of environmental situations. Possibly the local populations would respond in some manner to the local conditions and evolve into distinctive populations. The Galapagos finches could have had a similar history. Long ago a few birds might have been accidently carried by winds or storms from the west coast of South America, where their closest relatives live today, to the Galapagos. There they spread slowly from island to island. This may have been a rare event since at the present time there seems to be little or no inter-island movement. Thus, each

island would have an almost completely isolated population and possibly it would slowly evolve so that each island would come to have its own variant—as with the tortoises. But how could they change?

Darwin was offering speculation and, for that period, rather wild speculation. He was saying that if evolution could occur it could account for the armadillos, tortoises, and finches.

A skeptical biologist would have observed that neither the hypothesis of creation nor of evolution could be validated. Both might seem reasonable—or wrong. There is, however, a fundamental difference between the two hypotheses: creationism is based on supernatural events that could never be studied by the methods of science; evolution is assumed to be based on natural phenomena that could, in theory at least, be studied by scientists. For those individuals deeply interested in answers to our original three questions, the research program seemed clear: study what can be studied with the procedures of science; reject creationism, not because it is wrong, but because it cannot be studied.

Darwin remained uncertain. A hypothesis of evolution was certainly plausible but the statements of science must be based on probability not plausibility. He was fully aware that the writings of Lamarck and Chambers on evolution were thoroughly discounted. Lyell was the foremost authority in geology and he had much to say on species as well. He had rejected evolution. The influences of fellow scientists were indeed powerful when essentially all rejected the notion of evolution. But more important than that, Darwin could not imagine what could be the mechanism of evolutionary change. How could one species possibly change into another? One practically had to enter the realm of supernatural phenomena to propose a way. Nearly all experience suggested what was called the *fixity of species*, that is, species do not change.

If one suspects that species are not fixed, proof must be given that one species can change into another. No one had ever observed such a thing and Darwin believed that the reason was that evolution is an exceedingly slow process. Yet if one was to consider seriously the hypothesis of evolution, a way to test it must be found. Remember the Morgan quote: "cherish those [hypotheses] that can be given an experimental verification and to disregard the rest, not because they are wrong, but because they are useless." With this point of view the notion of evolution was useless—but so was creationism.

A mechanism for evolutionary change: the hypothesis of evolution by natural selection

We have been discussing the Darwin of the late 1830s—two decades before he published the *Origin*. He was unable to make much progress in understanding the basis of variation or adaptation simply because he could not think of a reasonable mechanism. But eventually he did and one of the most interesting things about his proposed mechanism is that the basic idea came not from fellow biologists or geologists but from a sociologist.

The Rev. Thomas Robert Malthus (1766–1834) published his important study, *An Essay on Population*, in 1798. Malthus was greatly distressed by the prevelance of human misery and poverty that he saw in England during those years of the Industrial Revolution. Why was there such misery? He suggested that the answer was to be found in the relation between the rate of human population growth and the rate of increase of the human food supply. He suspected that people were outbreeding the crops and the inevitable consequence would be not enough food for all. Thus, misery and hunger are inexorable consequences of being human. There has always been starvation and probably always would be unless human beings changed their reproductive behavior. Malthus suggested that all life has the same problem:

> Through the animal and vegetable kingdoms, nature has scattered the seeds of life abroad with the most profuse and liberal hand. She has been comparatively sparing in the room, and the nourishment necessary to rear them. The germs of existence contained in this spot of earth, with ample food, and ample room

> to expand in, would fill millions of worlds in the course of a few thousand years. Necessity, that imperious all-pervading law of nature, restrains them within the prescribed bounds. The race of plants, and the race of animals shrink under this great restrictive law. And the race of man cannot, by any efforts of reason, escape from it. Among plants and animals its effects are waste of seed, sickness, and premature death. Among mankind, misery and vice.

Darwin tells us that this suggestion of Malthus was the key that he sought—a mechanism for evolutionary change. He was well aware of variation among the individuals of a species—in minor ways to be sure. Some might be large, others small; some with one color pattern, others with a different pattern; some with long hair, others with short hair. So far as he could tell, there is no reason to suspect that every character might not vary. If some of the variant characters better adapt the individual to surviving and leaving offspring, wouldn't it be reasonable to suppose that, over the course of time, individuals of the better adapted type will make up most and eventually all of the population? They would simply outbreed the less adapted types of individuals.

Thus the normal variation that all naturalists agreed characterized species in nature would allow nature to select the "better" variants and slowly the species would change. Darwin referred to this phenomenon as *natural selection* and hypothesized that it could be the long sought mechanism of evolutionary change. Evolution was an ancient idea; natural selection was a new idea. Darwin realized that he had to make a case for natural selection, and if he could, the hypothesis of evolution would become more likely. The title of his book contained a statement of his hypothesis: *On the Origin of Species by Means of Natural Selection, or the Preservation of the Favoured Races in the Struggle for Life.*

This hypothesis is testable, hence useful. We will now formulate a series of deductions and seek to test them.

Deduction 1: *If the hypothesis of evolution by natural selection is true, there must be variation among organisms*

This deduction can be tested by finding out whether or not there is variation among the individuals of a species. The first two chapters of the *Origin* provide the evidence known to Darwin concerned with this deduction.

It comes as a surprise to many to learn that the *Origin* begins not with the phenomenon of variation of organisms in nature but under domestication. There was a good reason for this. The first sentence of Chapter 1 reads:

> When we look to the individuals of the same variety or subvariety of our older cultivated plants and animals, one of the first points which strikes us, is, that they generally differ much more from each other, than do the individuals of any one species or variety in a state of nature (*Origin*, p. 7; unless otherwise noted all references are to the first edition).

Darwin could be confident that most of his readers would be familiar with the dramatic variation shown by most cultivated plants and domesticated animals. In the 19th century there was a great deal of interest in England in selecting new varieties of domesticated plants and animals. The results could be striking. Notice how Darwin emphasized that the selected varieties "generally differ much more from each other, than do the individuals of any one species or variety in a state of nature." Darwin was planting the notion that selection could be both quick and powerful in producing variations. His readers might not be aware that there was variation, albeit less, in wild populations. Thus he was wise to begin his argument with the familiar.

Darwin was also planting the idea that all differences need not be the consequence of Divine Creation. He could be sure that no reader would believe that Creation was the reason for the new breed of sheep or for a better beet. It would be accepted that the cultivated varieties were the product of *artificial selection.*

> The great power of this principle of selection is not hypothetical. It is certain

> that several of our eminent breeders have, even within a single lifetime, modified to a large extent some breeds of cattle and sheep (*Origin*, pp. 30–31).

Darwin felt that artificial selection was a model for natural selection, the difference being in the agent responsible. In one case nature selected what was "better" for survival and the production of offspring. In the other, man selected what was "better" for his purposes: cows that produced more milk, hens that had more breast meat or laid more eggs, roses that were more beautiful.

Darwin studied the various breeds of domestic pigeons and used them as an example of the amazing amount of variation that is possible.

There was no doubt that variation under domestication is a fact. This is so certain that to qualify it with the phrase "beyond a reasonable doubt" would be just plain silly. What about variation in nature? After all, Darwin was interested mainly in the possibility of evolution in nature, not in the barnyard. But he came to see the two as but aspects of the same forces.

There is a tremendous amount of variation in nature. Darwin had been impressed by this while on the Beagle expedition. Later he combed the publications of fellow scientists for additional facts. He found variation not only in superficial external features but in internal structures as well.

> I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure, which he could collect on good authority, as I have collected, during a course of years (*Origin*, p. 45).

The most important point about variation in nature for Darwin was the fact that there seemed to be a continuous array of cases: from two populations being essentially identical; to two being slightly different, but sufficiently so for naturalists to classify them as two varieties; with greater differences they would be recognized as different subspecies; and finally so distinctive that each population would be classified as a "good" species.

> Certainly no clear line of demarcation has as yet been drawn between species and sub-species—that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. *These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage* (*Origin*, p. 51; italics mine).

Thus, Darwin found ample and convincing evidence of variation in populations of organisms, both in nature and in domestication. Therefore the deduction is correct and the hypothesis of evolution by natural selection becomes somewhat probable—at least it has not been falsified.

Deduction 2: *Natural selection can be operative only if more offspring are born that survive*

The idea that only a few of the many offspring of animals, or of the many seeds of plants, survive, was again something that Darwin's readers would know or suspect. They might also have observed that the population size of organisms seems to remain about the same year after year. A single oyster produces millions of egg each year yet the sea does not fill with oysters. A single oak tree can produce thousands of seeds each year yet, in natural areas, the number of oak trees remains about the same.

> There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair. Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny . . . . The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three

> pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair (*Origin*, p. 64).

Yet, in the likelihood, an average original pair would have only two surviving offspring—14,999,998 would not have made it. Thus, the *Struggle for Existence* is a tremendously impressive fact of nature.

> It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage (*Origin*, p. 63).

Thus, the deduction that more offspring are produced than can survive can be accepted as true. The hypothesis of evolution by natural selection is not falsified by this test and, hence, becomes more probable.

Deduction 3: *If the hypothesis of evolution by natural selection is true, there must be differences between the offspring that survive and reproduce and those which do not*

"Selection" implies that some individuals are chosen and others are discarded. An animal breeder can not develop a new variety of sheep, with heavier fleece for example, if he lets all the individuals in his flock reproduce. Success could only be assured if he kept the lambs of parents with the better fleece and sent all the other little lambs to market.

Similarly in nature if it is a matter of chance or luck which perish and which survive there would be no selection. What evidence did Darwin have to offer on this important deduction, which is the very heart of the concept of natural selection? He could make an effective case for the reality of artificial selection and suggested that the same general principle could hold in nature as well. But was there any evidence?

> It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into the long past geological ages, that we see only that the forms of life are now different from what they formerly were (*Origin*, p. 84).

Darwin rested his case on this logical argument, not data. There was no critical evidence that demonstrated a difference between the offspring that survived and those that perished. Compelling as the logical argument might be, the hypothesis of evolution by natural selection would be iffy until evidence for the reality of natural selection could be offered. Nevertheless, the inherent logic of the argument was sufficient for many 19th century naturalists.

Even to this day, the demonstration of natural selection remains difficult except in certain special situations. Darwin himself realized that demonstration would be most difficult for he believed that "we see nothing of these slow changes in progress, until the hand of time has marked the long lapse of the ages . . . ." And he felt sure that those ages were considerably greater than the life span of any human observer. So it would never be possible for a scientist to observe one species evolving into another.

Today this is how we view the situation. Since natural selection has been operating on natural populations continually, any genetic variant that could be classed as "good" would surely have appeared at some time in the past and have been screened by selection. Thus, the populations that we see today are the best that selection has been able to accomplish with the genetic variants that have appeared to date. The chance of any observer being lucky enough to detect a truly new genetic variant in a natural population under natural conditions that would be "better" is extraordinarily slight.

The deduction was eventually tested by

other means and shown to be correct. The most dramatic evidence comes from situations in which a population is presented with an environmental challenge never before encountered and, hence, never before selected for. Examples are insects sprayed with pesticides and microorganisms exposed to antibiotics. When the population encounters this new environment, for which they are clearly not adapted, there may be a rapid evolution of resistance.

More will be presented later on the modern evidence for the reality of natural selection. That evidence came a century after Darwin and hence was not available for him to answer his critics.

Deduction 4: *If the hypothesis of evolution by natural selection is true, only those variations that are inherited will be important*

In Darwin's time the relation between the characteristics of individuals and their inheritance was poorly understood. It was obvious, of course, that much was inherited: the offspring of chickens were chickens, not pigeons. On the other hand some of the minor differences among a flock of chickens might be passed to the offspring and some not. Some of these minor characteristics might then reappear after several generations. If that was the case, was the variant new or had it been transmitted but in a dormant state—whatever that might mean.

> Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part differs, more or less, from the same parts in the parents (*Origin*, p. 167).

These confusing aspects of inheritance were especially notable, and noticed, in human families. At times twins would be of the same sex and be remarkably alike in appearance and in personality. At other times twins might differ in sex and characteristics or be of the same sex and still differ in appearance and personality—being no more alike than brothers and sisters born one at a time.

In 1859 there was simply not enough information about inheritance to provide the necessary foundation for the hypothesis of natural selection. Darwin realized that this was a critical lack and nine years later, in 1868, published a two volume work on inheritance: *The Variation of Animals and Plants under Domestication*. Most of the data were extracted from the literature and they varied from reliable to totally unreliable observations and it was not possible to tell which was which.

Neither Darwin nor or anyone else was able to account for the origin, or apparent origin, of new variations. Darwin assumed that new variations were related in some way to the environment but not in a Lamarckian sense—that is, he did not believe that the environment induced specific adaptations (long hair in cold climates, etc.). The best that Darwin could do was to conclude:

> Whatever the cause may be of each slight difference in the offspring from their parents—and a cause for each must exist—it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted survive (*Origin*, p. 170).

Although Darwin accepted that there could be new variations appearing in populations, there was great uncertainty on the part of many scientists that these variations could be of sufficient magnitude to enable one species to evolve into another. All sorts of bizarre traits had been selected to produce a bewildering variety of breeds of pigeons—*but they were all pigeons*. Even the most extreme breeds could be crossed and produce fertile offspring. Ability to cross and produce fertile offspring was the generally accepted test for good species at that time. Darwin had emphasized earlier that some of the breeds of dogs, for example, are as different in structure and behavior as different wild canine species, but they still could be crossed. Nevertheless, no arti-

ficial selection had produced a "new species."

One of Darwin's critics, Fleeming Jenkin (1867), suggested that new variants could never produce any lasting effect. His was a most telling argument. If a new variant arose in a population, according to Jenkin, it would of necessity have to cross with the other members of the population. When different varieties were crossed it was accepted that *blended inheritance* was the rule. That is, the offspring would be intermediate. So, the offspring of the variant and a regular individual would be intermediate. Their offspring would, most likely, breed with the regular forms again so the next generation would be even more like the regular individuals. Thus, any new variations would be expected to be diluted and disappear. That would be the consequence if blended inheritance was the rule—and in Darwin's time that was accepted as one of the few sure things that could be said about inheritance. Thus, Jenkin's argument was a telling blow to the Darwinian hypothesis. It was telling, however, because it was thought to be valid. Now we know better. Inheritance is not a matter of blending the differences of the parents—but Mendel was still a half-century in the future.

Thus Darwin was not able to confirm the validity of Deduction 4 that the variations which are important in evolution are inherited. (But the deduction did seem highly probable and eventually convincing data were accumulated.) This, coupled with the fact that Deduction 3—the attempt to demonstrate natural selection in nature—could likewise not be confirmed, led many scientists to have serious doubts about the hypothesis that natural selection is the mechanism for evolutionary change.

At the same time the number of scientists and others who came to accept evolution increased. To them Mr. Darwin had made his point about the possibility of evolution, he just did not know what made it happen. But in retrospect, Huxley (1888, p. 197) maintained "the *Origin* provided us with the working hypothesis we sought."

What, then, was the basis for the acceptance of the hypothesis of evolution as the answer to our questions about organic variety and adaptation? The answer lay hidden in the rocks.

The critical information required for proving the hypothesis of evolution is data on the conversion of one species into another. Evolution means descent with change, so it would be necessary to show that ancestors and descendants are in fact, different. On the face of it, that sounds like a nearly impossible task. Remote ancestors are remote and hence not available for direct study. Nevertheless, the hypothesis of evolution, no matter how logical it might seem, would remain in doubt unless some means of reconstructing the past history of life exists. So one of our most critical deductions will be:

Deduction 5: *If the hypothesis of evolution is to be established as true, we must be able to obtain information on organisms that lived in the past*

The data for this deduction were already available to Darwin. The rocks of the earth's crust held the secrets of many events that occurred in the past. Long-cooled lava flows told of ancient volcanic eruptions. Limestone told of ancient sea bottoms where the sediments were slowly changed to rocks. Smooth horizontal rocks, with parallel grooves, told of ancient glaciers that had ground across them. The depths of canyons gave some idea of the length of time that it must have taken rivers to cut them.

Evidences of past life were to be found in one of the two basic kinds of rocks. The granites and lavas are formed by the cooling of molten rock from the interior of the earth. These are the *igneous rocks.* The horizontal layers of rock that form such a conspicuous feature of cliff faces in many parts of the world are the *sedimentary rocks.* These layers, or strata, of sedimentary rocks start as material settling at the bottom of a lake, inland sea, or ocean; or are deposited on land by wind or eroding waters. Gradually these deposits are covered and the buried ones slowly change to stone. This method of formation means that the topmost deposits of sediments are the most recent

and the lowest layer the oldest. If these deposits happen to include the remains of animals or plants, these may be fossilized—changed to stone. Thus the sedimentary rocks are time capsules of earth history. Each stratum contains information about events occurring at the time of its formation.

The possibility of the remains of a dying organism being fossilized is exceedingly remote. Most dead organisms are quickly consumed by other organisms. Organic compounds and the energy they contain are too valuable to be wasted in nature. If the organism has hard parts: shells, teeth, bones, or an exoskeleton, there is a better chance of these structures surviving rapid destruction—and hence the chance of their fossilization increases.

But fossils do occur so we have the possibility of learning something about life in the past that could throw light on whether or not evolution has occurred. Thus, we can become somewhat bolder in formulating our deductions since the past is not closed to study.

Deduction 6a: *If the hypothesis of evolution is true, the species that lived in the remote past must be different from the species alive today*

The basic idea in evolution is that natural populations slowly change over long stretches of time and, therefore, ancestors and descendants will, of necessity, be different from one another.

Once again, the data to evaluate the deduction were available to Darwin and other naturalists: fossils had been known for a very long time. A few fossil species proved to be very similar, or even identical, with living species but the vast majority were very different from life today. Especially striking and interesting were the remains of some of the vertebrates, whose bony skeletons increased their chances of being fossilized. There were huge elephant-like creatures that had lived on land and monstrous reptiles that had lived in the sea. There were spectacular plant remains such as the giant tree ferns and many other species entirely different from any alive today.

Thus it was true beyond a reasonable doubt that few of the species alive today occur also as fossils in the remote past. The vast majority of the fossil species are no longer with us. The deduction is shown to be true so the hypothesis of evolution is made more probable.

We can continue with a similar but more sophisticated deduction.

Deduction 6b: *If the hypothesis of evolution is true, the older the sedimentary strata, the less the chance of finding fossils of contemporary species*

Testing of this deduction will involve not only finding fossils but knowing something about the time they lived. In the middle of the 19th century there were no accurate methods for determining the ages of the strata of sedimentary rocks. Nevertheless, it was possible to obtain data that allowed a test of Deduction 6b. If we are looking at the face of a cliff of sedimentary rocks, the layers will generally be more or less horizontal and we have seen that the bottommost layer will be the oldest and the topmost the youngest. For Deduction 6b we need not know whether the oldest layer is a million, ten million, or a hundred million years old. Such data would be fine to have but all we need to know is relative age and this can be determined by the position of the layer relative to other layers. If the deduction is correct and if the layers are relatively young (geologically speaking), we should find more fossils of still-living species in the topmost layer and fewer in successively lower layers.

This hypotheses was first tested by the famous English geologist and friend of Charles Darwin, Sir Charles Lyell (1797–1875), and by a French geologist, Gérard Paul Deshayes (1797–1875). They collected fossil shells from different strata that had been formed in a geological era known as the Tertiary. The oldest strata had been given the name Eocene and the most recent Pliocene. These divisions of the Tertiary are shown in Figure 1, which is the modern geological time scale. Table 1 gives the data. Nearly all of the Recent Pliocene fossils belong to species still alive whereas almost none of the Eocene fossils do. The deduction has been tested and found to be true,

so we can say that the hypothesis of evolution becomes even more probable.

The finding that progressively older strata have progressively fewer species that are alive today is not what one would expect from the hypothesis of Divine Creation. If all species of animals and plants had been created within four days, as a literal interpretation of Genesis I demands, all strata might be expected to have the same array of fossils. That is most definitely not what the geological record shows. Nevertheless, Lyell's data do not prove that Divine Creation did not occur—if supernatural forces are invoked, anything can be explained. What one could say, however, is that if we accept as valid evidence only what we can observe and employ only the naturalistic methods of science, the hypothesis of evolution is more probable than the hypothesis of Divine Creation. Science as a way of knowing was proving to be a powerful method of gaining an understanding of the natural world.

Deduction 7: *If the hypothesis of evolution is true, we would expect to find only the simplest organisms in the very oldest fossiliferous strata and the more complex ones to appear in more recent strata.*

Some cautionary remarks must be made about this deduction. Evolution means change—not necessarily becoming more complex. Some species alive today, many parasites for example, may be simpler structurally than their ancestors. Nevertheless, Darwin and other evolutionists assumed, as we do today, that the very earliest forms of life must have been small and simple and that slowly, very slowly, more complicated species evolved.

During the first half of the 19th century, geologists developed a time scale that forms a framework for discussing the past. The basic data consisted of measuring the thickness of the sedimentary strata and arranging them in a sequence from the oldest to more recent. This is the *geological column.* Even on the basis of the strata known at the time, the geological column turned out to be dozens of miles thick. Of course, this huge pile of rocks was not observed in any one locality. Sedimentary rocks are not formed as a uniform layer across the earth's crust but, at any specific period of time, deposition will occur in one restricted region; later it will occur elsewhere. By examining all the available cliffs and railroad cuts, it was eventually possible to put the pieces of the puzzle in place and be able to arrange all of the strata in a composite column of rocks.

TABLE 1. *Percentages of Tertiary species still living. Data from Lyell (1854, pages 389–395).*

	Fossil species	Alive today	Percent of fossil species still alive
Recent Pliocene	226	216	96
Older Pliocene	569	238	42
Miocene	1,021	176	17
Eocene	1,238	42	3

The early work on accumulating the data for the geological column was done in England at the time of the Industrial Revolution. One of the important activities then was the linking of all parts of England, Wales, and Scotland by railroads. The railroad builders frequently had to cut deep pathways through hills. This afforded the geologists a wonderful opportunity to observe strata in places where, otherwise, they would have been covered.

When first devised the geological column measured only relative time. That is, the lower the stratum, the older it was. Absolute geological time became known only after the radioactive methods for dating became available in the early years of the 20th century. A modern version of the geological column is shown as Figure 1.

Even in the early years of the 19th century, geologists realized that the oldest strata contained simpler forms—invertebrates alone were found. Only later did higher vertebrates—reptiles, birds, and mammals—appear. The same was true for the plant kingdom. Algae, mosses, ferns and similar plants were very old; the angiosperms were more recent. In 1824 Lyell (1826, p. 513) had this to say:

> An opinion was entertained soon after the commencement of the study of organic remains, that in ascending from the lowest to the more recent strata, a

TIME FROM BEGINNING	ERA	PERIOD Epoch
	CENOZOIC	QUARTERNARY
0.01		Recent
1.8		Pleistocene
		TERTIARY
6		Pliocene
25		Miocene
38		Oligocene
55		Eocene
65		Paleocene
140	MESOZOIC	CRETACEOUS
180		JURASSIC
230		TRIASSIC
280	PALEOZOIC	PERMIAN
350		CARBONIFEROUS
400		DEVONIAN
430		SILURIAN
500		ORDOVICIAN
550		CAMBRIAN
670		EDIACARIAN
2,500	PROTEROZOIC	
4,600	ARCHEAN	

FIG. 1. A modern version of the geological time scale. Time in million years.

TABLE 2. *Time and life. The data for 1852.*

Cambrian	No reliable evidence of life; "a few obscure traces of fossils have been detected."
Silurian	No land plants. Oldest fossil fish. Many invertebrates: trilobites, graptolites, brachiopods.
Devonian	No reptiles. Many fish, some with armored plates (the ostracoderms).
Carboniferous	Many invertebrates. Oldest known reptiles.
Permian	More reptiles.
Triassic	Reptiles and batrachians. Horsetails.
Jurassic	Large reptiles such as pterodactyls, plesiosaurs. Cycads, conifers, ferns. A few palms. First mammals.
Cretaceous	Mostly marine fossils. Reptiles, many invertebrates.
Eocene	Mediterranean-type plants. Many mammals but all are of extinct species. Nearly all shells are of extinct species.
Miocene	All the mammals and about two-thirds of the shells are of extinct species.
Pliocene	About the same.
Recent	All of the shells and many of the mammals are of living species. First human remains.

> gradual and progressive scale could be traced from the simplest forms of organization to those more complicated, ending at length in the class of animals most related to man [i.e. the mammals].

In the 1820s one had to be cautious—after all, very little paleontological work had been done. Much more was known in the 1850s when Lyell's *Principles of Geology* was first published. His *Manual*, which contained the data on paleontology that had been removed from later editions of the *Principles*, appeared in its fourth edition in 1852—a few years before the *Origin*. By then the data were much more convincing. Some of them are shown in Table 2.

Darwin and others at mid-century spoke of the inadequacy of the geological record. In many ways it was inadequate since relatively few geologists had explored the

strata in only a small part of the world. Nevertheless, the record was sufficiently adequate to test Deduction 7. It was true beyond a reasonable doubt that there had been a progression of forms of life, with the less complex species appearing before the more complex. The various kinds of invertebrates were well represented at the very beginning of the fossil record in the Silurian; the mammals were first encountered in the much younger Jurassic strata. Thus the hypothesis of evolution becomes more probable.

Essentially all of the prominent geologists in the pre-*Origin* years were creationists. One was Lyell who made the first grand synthesis of geological data and he saw the progression of life. He fully realized that each major group of strata had its own distinctive life forms—many not known in either younger or older strata. How could a creationist explain such facts? The great French anatomist and geologist Cuvier (1769–1832) had suggested that there had been a series of creations and extinctions. His hypothesis explained the data of the early 1800s as well as did the hypothesis of evolution.

Darwin's hypothesis was radically different from Cuvier's. For Darwin the species at any one period of earth history were the progenitors of the species of all subsequent periods. There was no break in the lineage of life. Presumably all forms alive today are the remote descendants of the first sorts of life that appeared on earth. Thus the most critical deduction of all will be:

Deduction 8: *If the hypothesis of evolution is true, it must be possible to demonstrate the slow change of one species into another*

Darwin failed. There were no critical data in the 1850s that showed the evolution of one species into another. Darwin thought that this was but a reflection of the inadequacy of the fossil record. In a sense he was correct but today, when we know so much more about speciation, we realize why it is exceedingly difficult to obtain convincing fossil evidence of the evolution of one species into another.

Darwin and others at the time were more interested in a related question: were there fossils that were intermediate between major groups of animals? Were there *missing links*, which if discovered, could document the evolution of life? This leads to another deduction.

Deduction 9: *If the hypothesis of evolution, which assumes that all of today's species are the descendants of a few original forms, is true, there should have been connecting forms between the major groups (phyla, classes, orders)*

> Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps is the most obvious and gravest objection that can be urged against my theory. The explanation lies, as I believe, in the extreme imperfection of the geological record (*Origin*, p. 280).

If that explanation was correct, one must assume that greater efforts by collectors of fossils would eventually supply the data. It was also possible to predict what sorts of fossils might be the most promising. The answer is the vertebrates. There are two main reasons for this. First, the bones and teeth of vertebrates are excellent candidates for fossilization. Second, the vertebrates—or rather the Phylum Chordata of which they are the principal representatives—are the most recently evolved of the major phyla. Many of the invertebrate phyla were already present in the then oldest known strata from which fossils had been collected—the Silurian rocks. What may have happened during earlier times could not be determined without fossil remains. This means that the common ancestors of any two of the phyla already present in the Silurian would have lived at an earlier time when no fossil record was then available. On the other hand, one could work with the bony chordates—the vertebrates. Of the major groups—fishes, amphibians, reptiles, birds and mammals—only the most primitive, the fishes, were present in earliest fossil-bearing strata. If, as Darwin imagined, all the other ver-

tebrates were evolved from fishes, there would be a chance of documenting his belief.

The first dramatic proof for the existence of fossils intermediate between major groups came in 1861—two years after the publication of the *Origin*. In a quarry near Solenhofen in Bavaria, a feather was discovered in strata of Jurassic age. Shortly thereafter a well-preserved specimen of a strange fossil was discovered and named *Archaeopteryx*. It was a confusing mixture of structural features of modern birds and primitive reptiles known as archosaurians. The skull was somewhat bird-like but the jaws contained teeth, characteristic of reptiles but absent in all modern birds. There was a long reptilian-like bony tail, in contrast with the modern birds which have the tail vertebrae fused in a short projection—the "tail" being feathers only. In fact, the skeleton was more similar to that of the archosaurians than to modern birds. Nevertheless, *Archaeopteryx* had wings and the entire body was covered with true feathers. It could be debated whether *Archaeopteryx* should be classed as a reptile or bird but, using the presence or absence of feathers as the main diagnostic feature, paleontologists classified it as a bird.

Of course this is exactly what would be hoped for in a "missing link"—a species so perfectly intermediate between two major groups that one could debate to which group it should be assigned. Darwin had assumed that birds must have evolved from primitive reptiles and here was the evidence that should have convinced many scientists that they had. *Archaeopteryx* remains today as one of the best examples of a link no longer missing. "Here was a truly intermediate form between the reptiles and the birds" (Colbert, 1980, p. 183). Another modern paleontologist (Ostrom, 1974) offers this opinion:

> *Archaeopteryx* represents a "main-line" or transitional organism between an archosaurian ancestor and all subsequent birds. Some critics may attack this premise on the grounds of improbability, but my response to that is a challenge for them to identify *any positive* anatomical evidence (in *Archaeopteryx* or any later bird) that precludes either archosaurian ancestry or the main-line position ancestral to later birds.

Here then was the "smoking gun" that Darwin and the other evolutionists required—a fossilized link between two major groups of vertebrates. This gave strong credibility to the hypothesis of evolution. One would have assumed, therefore, that intense enthusiasm would follow such a discovery. Surprisingly, this was not the case.

The specimen discovered in 1861 was sent the the British Museum (Natural History) in 1862 and was studied immediately by the famous English anatomist Richard Owen (1863). It was restudied by Huxley (1868). Neither saw in *Archaeopteryx* the importance we ascribe to it today. In the fourth edition and later editions of the *Origin*, Darwin gave a single entry in the index for *Archaeopteryx*. There we read only that a

> strange bird, the Archaeopteryx, with a long lizard-like tail, bearing a pair of feathers on each joint, and with its wings furnished with two free claws, has been discovered in the [Jurassic] slates of Solenhofen (*Origin*, 1892, p. 266).

There is another mention however that first appeared on page 284 of the fifth edition:

> Even the wide interval between birds and reptiles has been shown by [Huxley] to be partially bridged over in the most unexpected manner, on one hand by the ostrich and extinct Archaeopteryx, and on the other hand by [one of the dinosaurs].

Archaeopteryx is not listed in the index of the five volumes of Darwin's letters (F. Darwin, 1888, 1903). In a lecture given in 1880, Huxley (1895*a*, pp. 234–235) saw and emphasized its importance. This was in his essay, "The coming of age of 'The Origin of Species'." He quoted Darwin's belief that there must have been links between birds and reptiles but that such a belief was not supported by evidence in 1859. Huxley continues.

> But the progress of knowledge has justified Mr. Darwin to an extent which could hardly have been anticipated. In 1862, the specimen of Archaeopteryx, which, until the last two or three years, has remained unique, was discovered; and it is an animal which, in its feathers and the greater part of its organization, is a veritable bird, while, in other parts, it is distinctly reptilian.

Slowness in recognizing the importance of a new discovery in science is far from being unusual. In science, as in other fields of knowledge, it is exceedingly difficult to put two and two together unless one already knows that the answer is four.

Thus the critical deduction that there must be forms intermediate between major groups of organisms could be satisfied in this one case. Is one enough? Only one was available to Darwin in his lifetime. Subsequently, and especially in the 20th century, other dramatic and more complete examples have been discovered. Some of these will be mentioned later. Nevertheless, the "missing links" tend to remain missing, but today we realize that there are compelling arguments for why this is so.

One final deduction will have to do with time. Darwin's *Origin* appeared during a period of history when most educated people assumed that the earth was not very old. Bishop Ussher's date of Creation as 4004 B.C. was so widely accepted that it was included in the King James Version of the Bible then printed. Nevertheless, geologists were coming more and more to the opinion that the earth was very old. Hutton (1788, p. 304) concluded his famous study, the *Theory of the Earth*, with this statement: "The result, therefore, of our present inquiry is, that we find no vestige of a beginning—no prospect of an end." Irrespective of Hutton's very considerable firsthand knowledge of geology, his statement was hypothesis, not fact.

Darwin knew that he needed vast ages if his hypothesis of evolution was to be accepted.

Deduction 10: *If the hypothesis of evolution is true, the age of the earth must be very great, possibly many millions of years old*

How could one possibly measure the age of the earth? Neither Hutton nor anyone since him has been able to look at the surface of the earth and find any evidence that at some period of time there was no earth and then, later, the earth came into existence. Even if one found such evidence, was there any way of saying when that origin of the earth had occurred? No. The answer had to be sought by indirect means.

The first crude estimates were based on the thickness of the strata. Geologists had become convinced that sedimentary rocks came from material that had been deposited, generally under water. If one knew the rate of deposition and the thickness of a group of sedimentary rocks, one could compute how long it had taken them to form. Then, if one knew the total thickness of all the sedimentary rocks, it would be possible to give a figure for how long it took for all sedimentary rocks to form. That would give a minimum estimate of the age of the earth but would not, of course, tell us whether the earth had an origin or had always been in existence.

None of these estimates could be made with any exactness. The rate of deposition of materials would depend on the rainfall, slope of the land, and the nature of the material being eroded—all of which might vary over long periods of time. A given stratum of rocks might be very thick in one place and thin in another. One could never be sure that all strata were known.

Nevertheless, geologists came to believe that the earth must be very old.

> A man must for years examine for himself great piles of superimposed strata, and watch the sea at work grinding down old rocks and making fresh sediment, before he can hope to comprehend anything of the lapse of time, the monuments of which we see around us" (*Origin*, p. 282).

The then known strata in Great Britain alone totalled 72,584 feet, or 14 miles thick. Darwin knew of an estimate for deposition by the Mississippi River: 600 feet in 100,000 years. Thus, each foot would represent 166.67 years. That would mean that the

known sedimentary rocks in Great Britain would have taken 12 million years to form. Yet an even longer time might have elapsed, as one might imagine that the great Mississippi River, draining much of the continent, would have a very high rate of deposition.

Various other ingenious methods were used to determine the age of the earth. The salinity of rivers flowing into the ocean was measured. Knowing that and the total amount of salt in the ocean, one could estimate how long it had taken the ocean to receive its salt. Another method consisted of making an assumption about the temperature of the earth at the time it was formed and then estimating how long it would take for it to cool to its present temperature. Whatever the method employed, it turned out that the earth must be very old. No method, however, was capable of giving a reliable answer.

In was not until the 20th century, and especially since 1940, that reliable methods for determining the age of rocks have been perfected. All of these depend on the rate of radioactive decay of materials in the rocks. One can now estimate the age of rocks with an error of only several percent. These are the data used in Figure 1.

Although an acceptably accurate method for dating rocks was not available to Darwin, it seemed true beyond all reasonable doubt that an almost inconceivable length of time had elapsed since the organisms that lay buried in the oldest fossiliferous rocks had lived, and the present.

Was Darwin right?

What is one to conclude? Was the hypothesis of evolution, as advanced in 1859, true beyond all reasonable doubt? Different minds answered this question in different ways. Darwin's data and arguments were so reasonable for some scientists that they assumed that he must be right. Huxley was one of these: "My reflection, when I first made myself master of the central idea of the 'Origin' was, 'How extremely stupid not to have thought of that!'" (Huxley, 1888, p. 197). Other scientists were unconvinced. Some were deeply antagonistic. The same varied reactions came from men of the church and men of state. Yet Huxley was able to write in the late 1880s that "even the theologians have almost ceased to pit the plain meaning of Genesis against the no less plain meaning of Nature."

Darwinism was the great revolution in biology in the 19th century. That evolution was the explanation of organic diversity, adaptation, and the scala naturae was accepted by essentially all biologists and geologists. There was more doubt, however, about natural selection being the primary mechanism of evolutionary change.

One of the great achievements of evolutionary theory was that after 1859 it began to "make sense" of an otherwise bewildering mass of data. That will be our next major topic but, first, some references to the subjects so far covered will be given.

A Darwinism bibliography

The literature pertaining to Darwin and his life and times is enormous. Some of the key references will be cited.

Freeman (1977) provides an invaluable listing of all Darwin's publications, including most of the reprintings.

Darwin first published his views on the origin of species in a joint paper with A. R. Wallace in 1858. This famous paper is reprinted in J. Moore (1957) and de Beer (1958).

The *Origin* was first published, on 26 November 1859, with a press run of 1,250 copies, by John Murray. The second edition appeared on 26 December of the same year. The third edition appeared in 1861, the fourth in 1866, the fifth in 1869, and the sixth in 1872. A few corrections were made thereafter. The one-volume Murray editions from 1878 through 1891 give the final text.

Peckham (1959) provides a variorum of all editions. This makes it possible to see how Darwin changed the wording in the five editions after the first. The index to the *Origin* is brief and inadequate for many purposes, but recent printings of the Harvard University Press facsimile of the first edition have an expanded index containing references to modern concepts. In addi-

tion, Barrett, Weinshank, and Gottleber (1981) have published a computer-generated concordance of the first edition. Information about most of the individuals and items mentioned by Darwin, usually without citations, can be found in Freeman (1978).

Darwin's first and in many ways his most popular book is an account of the voyage of the Beagle (1839). It has been reprinted innumerable times. Some references dealing with the book and voyage are: Moorehead (1969), Marshall (1970), Barlow (1933 and 1954), Mellersh (1968), and Thomson (1975).

Many of Darwin's shorter papers have been made available in convenient form by Barrett (1977).

In recent years many of Darwin's notebooks and draft manuscripts, never intended for publication, have been issued: the essays of 1842 and 1844 (F. Darwin, 1909*a*; de Beer, 1958*a*); the Beagle diary (Barlow, 1933); the Red Notebook from the last year of the Beagle (Herbert, 1980); the manuscript on natural selection, intended to be part of a very large work of which the *Origin* was an abstract (Stauffer, 1975); the journal (de Beer, 1959*a*); notebooks on the transmutation of species (de Beer, 1960*a*–1967); ornithological notes (Barlow, 1963), notes and letters (Simpson, 1950).

General accounts of Darwin and his theory are Mayr (1982), Eiseley (1958), Ghiselin (1969), J. C. Greene (1959), J. Huxley and Kettlewell (1965), de Beer (1964), Ruse (1981), Irvine (1955), Allan (1977), Lanham (1968), Stone (1980—an historical novel but accurate), S. A. Bell (1959), C. D. Darlington (1959) and Appleman (1970).

Some of the 19th century accounts of Darwinism are Wallace (1870, 1889), Romanes (1892–1897), Poulton (1896), Jordan (1898), Gray (1876), LeConte (1891), Tyndall (1874), C. Darwin (1868, 1870), Schmidt (1873), Winchell (1871), Depéret (1909), Joly (1891), Vernon (1903), and T. H. Huxley (all citations except 1868).

Most of Darwin's fascinating letters seem to have been published. Often he expressed himself more openly in them than he cared to do in print. The more important of them, together with much general information, were published by his son, Francis Darwin (1888, 1903). Others have been published by Barlow (1967), Carroll (1976), F. Darwin (1909*b*), de Beer (1959*b*, 1960*b*, 1968), Litchfield (1915), Lowenberg (1939), Stecher (1961, 1969).

Some of the more personal insights are provided by Ashworth (1935), Atkins (1976), British Museum (1909), Raverat (1952), Irvine (1955), Eiseley (1958), Stone (1980), Osborn (1928), Gruber (1981) and by his autobiography (F. Darwin, 1888, vol. 1, ch. 2; Barlow, 1958, the complete version; Simpson, 1950).

For Darwin's close friend Charles Lyell see L. G. Wilson (1970, 1972), Bailey (1963), and Mrs. Lyell (1881). For Alfred Russel Wallace see Marchant (1916), F. Darwin (1909*b*), McKinney (1972), George (1964), Osborn (1928), and Williams-Ellis (1966). For Thomas Henry Huxley see Bibby (1959), Irvine (1955, 1960), L. Huxley (1900), and Osborn (1928). In the United States one of the most effective supporters of Darwin was Asa Gray. See Dupree (1959). His most outspoken opponent in the United States was Louis Agassiz. See Lurie (1960).

For the 19th century geological background, Lyell's books are fundamental. The three volumes of the *Principles* were published from 1830 to 1833. In 1838 he removed most of the historical geology from the *Principles* and published it separately as *The Elements of Geology*. In 1851 this was revised as the *Manual of Elementary Geology*. By 1853 the *Principles* was in its ninth edition and it ended with the twelfth of 1875.

Other sources for information on 19th century geology are: Playfair (1802), Buckland (1836), Dana (1863), Miller (1851–1860), Reingold (1964), Osborn (1931), Mather and Mason (1970), Schuchert and LeVene (1940), Merrill (1924), Lanham (1973), Adams (1938), Bailey (1963), Geikie (1905), Gillispie (1951), J. C. Greene (1959), M. T. Greene (1982), Ostrom and McIntosh (1966), and L. G. Wilson (1972).

For students who are not science majors

useful references are J. C. Greene (1959), Barlow (1958), Irvine (1955), Stone (1980), Eiseley (1958), Moorehead (1969), Raverat (1952), Gillispie (1951), and especially Gould (1977, 1980, 1983).

For general criticisms, including the religious reactions in the 19th century (the 20th century creationist controversy will be discussed later), see Glick (1972), Hooykaas (1972), T. H. Huxley (1888, 1895*a–f*), Kogan (1960), Mivart (1871), Irvine (1955), Mayr (1982), Rogers (1973), Russett (1976), R. J. Wilson (1967), Draper (1894), Hofstadter (1955, 1963), Hull (1973), Turner (1974), Ellegård (1958) and A. D. White (1896).

Some human interest episodes. Darwin's theory of evolution raised fundamental intellectual and emotional problems for many people. Some of the episodes may prove interesting for your students to explore. Here are some suggestions:

The famous debate between Huxley and Bishop Wilberforce at the Oxford meeting of the British Association on June 30, 1860 is described in F. Darwin (1888, vol. 2, pp. 320–322).

Lyell, the master of time and life, was slow to accept Darwin's hypothesis. A comparison of the different editions of his *Principles* and *Manual* would prove of interest. See also L. G. Wilson (1970, 1972), Bailey (1963), and Mrs. Lyell (1881).

Huxley and Prime Minister Gladstone had numerous debates in the press. One of the more fascinating was about the biblical story of the Gadarene swine (Matthew 8: 28–33; Mark 5: 2–13; Luke 8: 26–39). See T. H. Huxley (1895*b*, essay V and 1895*f*, essays X and XI).

The two American biologists, Asa Gray and Louis Agassiz, were pro and con on the issue of Darwinism. Dupree (1959) and Lurie (1960) can be consulted to see why.

A. R. Wallace independently came to the same conclusion about natural selection as had Darwin—before Darwin had published. For the solution of this problem—who should receive credit for the discovery—see F. Darwin (1888, vol. 2, ch. IV), Barlow (1958, pp. 121–122) and Moore (1957, pp. 342–344).

Darwin was ill for much of his life after he returned from the Beagle voyage. Winslow (1971) and Colp (1977) have speculated on the causes.

And, of course, there has been much speculation on Darwin's religious views. See F. Darwin (1888, vol. 1, pp. 304–317) and Gillespie (1979).

Now back to the main line of the argument.

"Nothing in biology makes sense except in the light of evolution"

The next five deductions will be grouped under the title of Dobzhansky's paper of 1973*a*. The great appeal of the theory of evolution for scientists in the last part of the 19th century was that it made so much sense out of an otherwise bewildering mass of data in biology and geology. By the last quarter of the 19th century, it was accepted by the majority of biologists and geologists that evolution was true beyond all reasonable doubt. It is proper, therefore, that we change its designation from "hypothesis" to "theory."

Apart from explaining the existing data, the theory of evolution proved of great value in directing the course of research. All important theories in science have this dual role—to explain the data already on hand and to suggest ways of acquiring additional information. Science is not only a way of knowing; it is also a way of discovering.

Dobzhansky's statement is likely to be accepted by scientists familiar with biology, yet we must admit that it does not make too much sense in and of itself. By implication, no other concept except evolution provides a satisfying explanation of biological phenomena. But surely the biology of Ray, Paley and the authors of the *Bridgewater Treatises* made perfect sense to them. For them "Nothing in biology made sense except in the light of Divine Creation." Natural theology can account for all of the phenomena of life to a degree of completeness that the Theory of Evolution can never achieve.

Nevertheless, natural theology came to be viewed as a sterile enterprise. The answer was always the same: "What is, is what was created." Supernatural powers

and processes, far beyond the ken of scientists to detect or study, explained all. After 1859 the more intellectually satisfying answer became: "What is, is what evolved." Nothing in evolutionary theory was beyond the power of scientists to try to study directly or indirectly. Some problems might be very difficult to study—for example, the history of life. For such information one had to be content mainly with fossils, fortuitously formed and fortuitously found. An additional glimpse of the past was possible when it was recognized that the species alive today have built into their gross and molecular structure evidences of their past history.

The modern mind, even of a fervent creationist, has the notion of biological relatedness so firmly embedded that we must remind ourselves of a fundamental difference between species that have been created and species that have evolved.

If each species had been created and remained in essentially the same form until the present, there could be no biological, or as we would now say genetic, relatedness among different species. Even the untutored mind recognizes a relatedness among dogs, wolves, foxes, and coyotes. Yet if each had been separately created they can be no more related to one another than any one of them is to a hippopotamus, dogfish, dodo, or oak tree. The biological, and usual, meaning of "related" is "connected by common ancestry." The separately created, constant through time, canine species could not have shared a common ancestry. Each species could have only creatures of its own kind for ancestors.

The new view that evolution brought was that canine species must have shared a common ancestor at some time in the remote past, and that over the ages, the ancestral population had split into separate lineages that led to the species as we know them today. On a larger scale, an evolutionist could suggest that all members of the Phylum Chordata are related in the sense that all share a common ancestor—some long extinct prochordate. If we accept this notion as worthy of analysis, we can view it as an hypothesis to be tested and formulate the following deduction.

Deduction 11: *If the members of a taxonomic unit, such as the Phylum Chordata, share a common ancestry, that should be reflected in their structure*

This notion—that the structure of all descendants from a common ancestor would show evidences of this descent—is based on the belief that modifications of the original structure would evolve very slowly. Hence, some of the original characters, or obvious modifications of them, must be present in the descendants. And of course if we put the putative descendants in the same taxonomic group, that means we recognize certain structural characteristics that they share.

Comparative anatomy was the discipline that first recorded the common characteristics of organisms in a systematic manner. This is not surprising since, at an earlier time, knowledge of physiology was rudimentary and cellular structure was unknown.

The Flemish anatomist Vesalius (1514–1564) put human anatomy on a firm footing in his *De Humani Corporis Fabrica* of 1543. Twelve years later a French naturalist Pierre Belon (1517–1564) published a book on birds. In it he showed, side by side, the skeletons of a bird and of a human being. The dramatic thing he did was to give the same names to the bones of the bird that had human counterparts. There was no difficulty, for example, in showing that two such apparently different structures—the bird's wing and the human arm—had corresponding bones.

Comparative anatomy was a major activity for biologists from the 16th to well into the 19th century. Skeletons received special attention. Not only were they more permanent than the soft tissues but, when the study of fossils became an active enterprise in the 18th century, the only possible comparisons of living and fossil species were of their bones.

The recognition of similar parts in different organisms is the concept of *homology*. For Belon in the 16th century and for later workers, the proximal bone of the human arm and of the bird wing are modifications of the "same thing." A skeptic could ask,

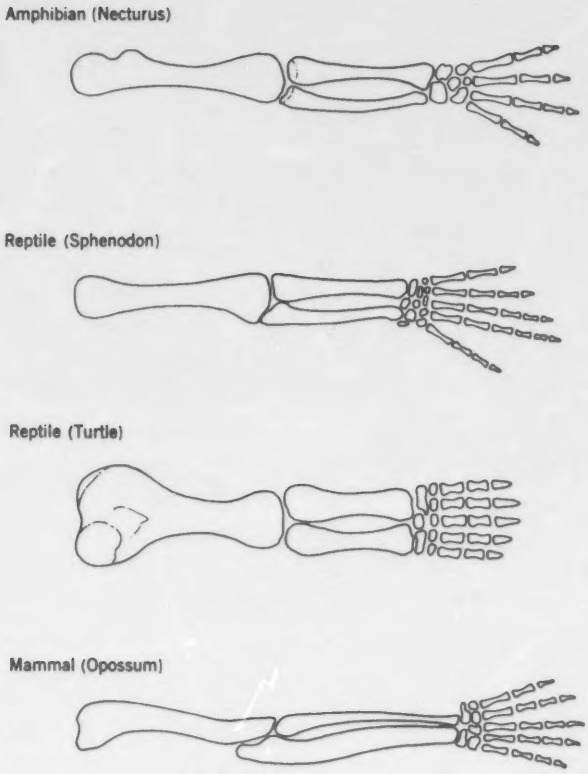

FIG. 2. The front limbs of four kinds of tetrapods.

"How could they be the same thing when they are parts of structures that differ so greatly in appearance and function?" The answer could only have been vague and unsatisfactory. But the concept of evolution made it obvious how the parts of birds and mammals could resemble one another: it would be held that the arm and wing are derived, through evolutionary modifications, from the anterior paired appendage of a common ancestor. Homology, then, is similarity based on common descent.

This explanation could be extended to suggest that the anterior paired appendages of all vertebrates—the pectoral fins of fishes, whales, and dolphins; the wings of birds, bats, and pterodactyls; the digging foreleg of a mole; the hoofed foreleg of horses and cattle; the prehensile arm of a sloth; and the tool-using hand of man—are examples of the same ancestral structure modified in different ways in different animals (Fig. 2). The driving force, according to the hypothesis, is natural selection acting on variation.

The Phylum Chordata has numerous splendid examples of how the concept of evolution made sense of the details of comparative anatomy. The data of comparative anatomy suggest that the living chordates can be arranged in ten subphyla and classes that indicate, in a very general way, increasing complexity: Hemichorda, Urochorda, Cephalochorda, Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, Mammalia. The first three are marine protochordates; the last seven are vertebrates. The Agnatha, Chondrich-

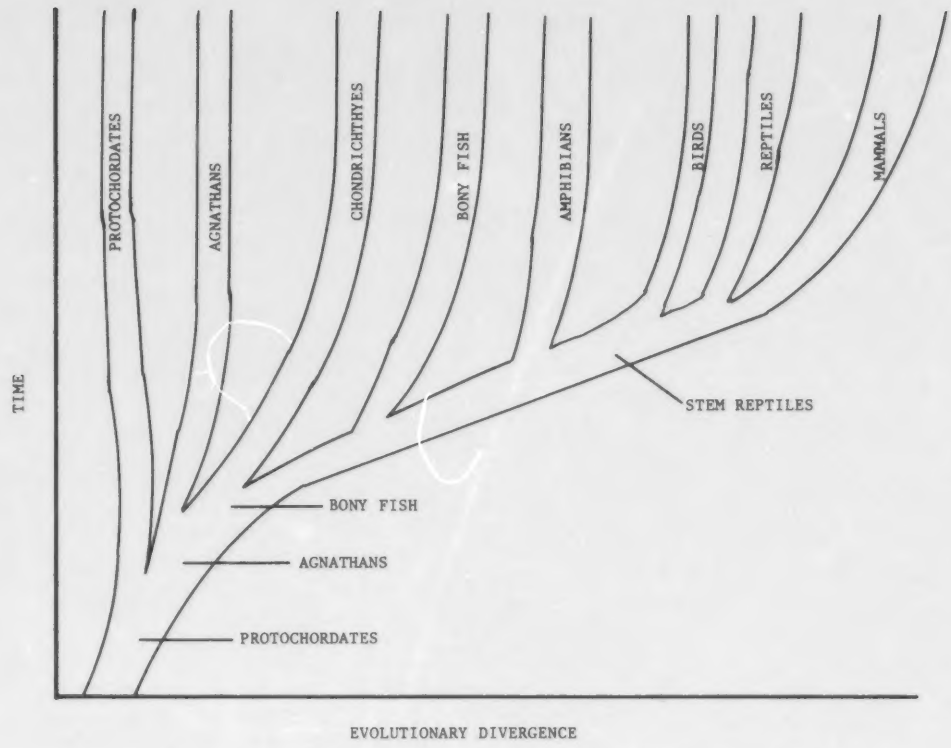

FIG. 3. The evolutionary relationships of the major chordate groups.

thyes, and Osteichthyes are fishes. The Amphibia, Reptilia, Aves, and Mammalia are tetrapods.

When the concept of evolution was applied, the data remained the same—only the interpretation changed. Biologists began to think of chordate evolution as a progression from very simple protochordates to the more complex birds and mammals. It seemed clear that different groups had split off the main line (the "main line" being that leading to us, naturally!) and to varying degrees had retained some of the characteristics of their ancestors at the time of the split. Thus the famous cephalochordate, *Amphioxus*, was looked upon as a relic of a pre-vertebrate stage of chordate evolution. The lamprey and hagfish of today, which differ so much in superficial appearances from the earliest known vertebrates, the ostracoderms, are so like them in fundamental ways that all are placed in the same class—the Agnatha. One can study living Agnatha, therefore, to learn something of a remote agnathan period of vertebrate evolution.

Slowly the paleontological data were obtained to show the broad outlines of vertebrate evolution. To a gratifying degree, the sequence that had been suggested by the data of comparative anatomy turned out to be the sequence of evolution. Figure 3 shows the broad outlines of vertebrate history.

Some of the classic examples of modification of parts that reflect evolution are jaws and ear ossicles, the arteries leaving the heart, the basic structure of all chordates, and the excretory organs. The first two will be described briefly now and the

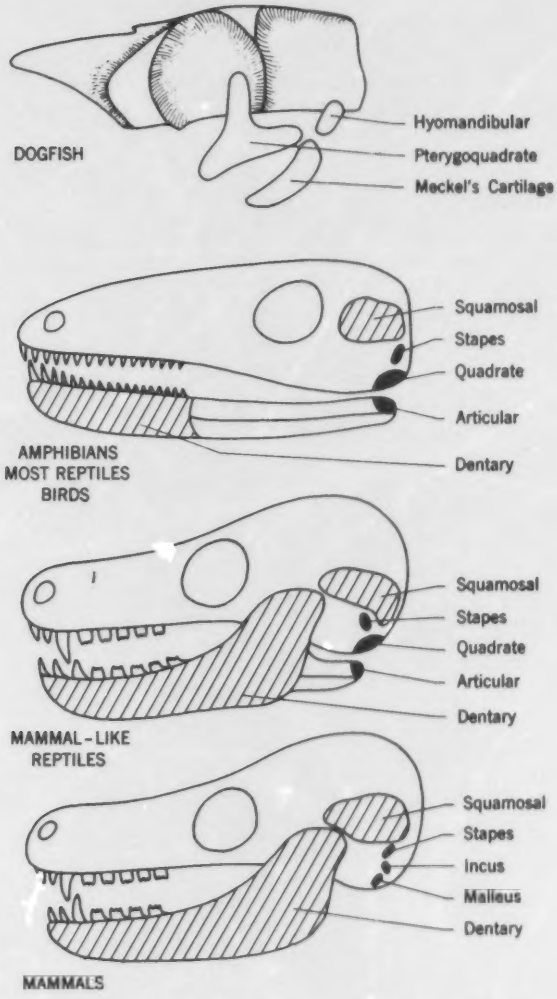

FIG. 4. The jaw articulation and ear ossicles of four vertebrates.

last two in relation to the next hypothesis, which concerns embryonic development.

Jaw joints and ear bones. The ear has two main functions in the vertebrates. In fishes it is an organ of balance only. In tetrapods the ear retains its function as an organ of balance but adds the detection of vibrations in air. The fishes lack both a tympanic membrane and ear ossicles. The living amphibians have one ear ossicle—the stapes—and, except for the urodeles, a tympanic membrane. Living reptiles and birds have basically the same structure as the amphibians. In mammals, however, there are two additional ear ossicles—the malleus and incus. What could be the origin of these ear bones?

A tentative answer was worked out almost entirely on the embryos of living vertebrates. Figure 4 tells the story briefly. Correlated with the formation of the "new" bone, *i.e.* the stapes in amphibians and the two "new" ones in mammals, there are important changes in the articulation of

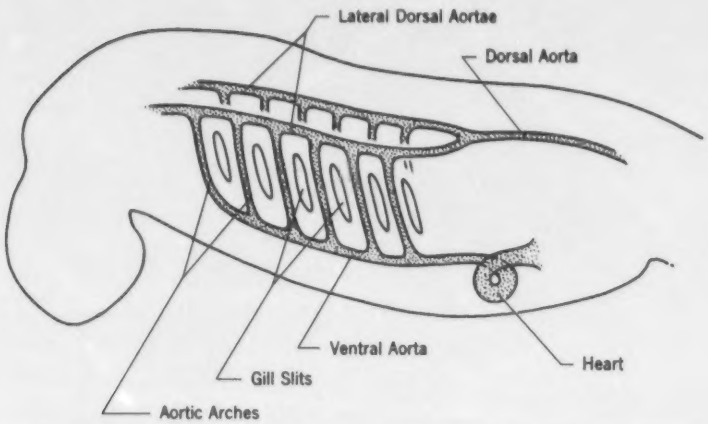

FIG. 5. The main arteries of the anterior trunk region of a vertebrate embryo.

the jaws. In the fishes the hyomandibular bone supports the jaws. The amphibian embryo has a hyomandibular but it becomes converted to the stapes of the adult. In a similar manner, the articular of the lower jaw and the quadrate of the upper jaw become reduced in size and move into the ear to form the malleus and incus of the mammals.

The hypothesis was advanced that these events in development might be a reflection of what had occurred in evolution. One would then deduce that at some stage in the past, presumably when reptiles were evolving into mammals, there would be evidence of the loss of the quadrate and articular as the jaw articulation and the modification of these bones into the incus and malleus. Concurrently, the jaw articulation must have switched to the mammalian pattern—the dentary of the lower jaw moving against the squamosal of the upper jaw. Now this suggests a very interesting and, seemingly, dangerous deduction for a paleontologist to make. Since there must always be some articulation point of the jaws if the animal intends to eat, how could there be a switch from the reptilian type to the mammalian type? It seemed unlikely that parents with the articular-quadrate joint would produce offspring with the dentary-squamosal type. But how else?

The answer was provided by the fossil synapsids, the mammal-like reptiles. As their name suggests, they are intermediate in structure between reptiles and mammals. In recent years a very large number of fossils has been found—mainly in South Africa. The different kinds show all gradations from the characteristic reptilian jaw articulation to that of the mammals. One genus from the Triassic is especially noteworthy. It was given the jaw-breaking name *Diarthrognathus*, which means "two-jointed-jaws," in recognition of the fact that it had two functional jaw articulations—reptilian and mammalian. One could not ask for a better intermediate between reptiles and mammals.

For more details on these dramatic discoveries see Goodrich (1930, ch. 8), Romer and Parsons (1977, pp. 480–483), Colbert (1980, pp. 136–137, 246–251), Hildebrand (1982, pp. 261–263), Young (1971, pp. 411–413; 1975, p. 124; 1981, p. 416), Romer (1969), Berrill (1955) and Luria, Gould, and Singer (1981, pp. 631–633).

The transformation of the aortic arches. The embryos of all vertebrates have a circulatory system of almost diagrammatic simplicity—in contrast to the confusing patterns among the adults. In the anterior part of the body there is a ventral vessel that carries blood anteriorly to the region of the gill slits (Fig. 5). There six pairs of aortic arches branch off and extend through the gill bars to the lateral dorsal aortae. The

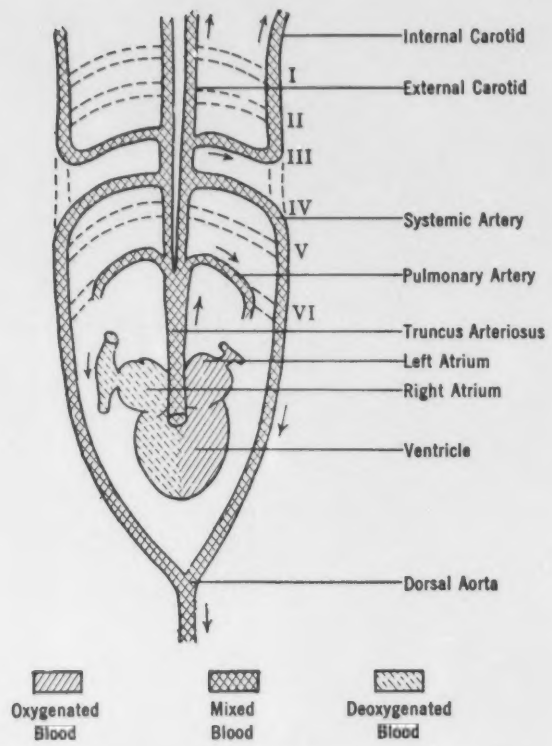

FIG. 6. The transformation of the aortic arches in a frog.

lateral dorsal aortae join posteriorly to form the dorsal aorta, which carries blood to all parts of the body behind the gill region.

This simple pattern of the embryo is transformed in very different ways in different vertebrates to produce the circulatory systems of the adults. Figures 6 and 7 provide two examples. In these two figures the point of view has been changed from that of Figure 5. If we were to look at the embryo of Figure 5 from below and spread the lateral dorsal aortae apart for clarity, we would end with the perspective of Figures 6 and 7.

The frog embryo passes through a stage with the six aortic arches. With further development some are lost or modified until the adult pattern as shown in Figure 6 is formed. The human embryo also has six pairs of aortic arches (never all at one time) and these become transformed (Fig. 7) but in a manner quite different from that of the frog.

For more details on the transformation of the aortic arches see Goodrich (1930, ch. X), Romer and Parsons (1977, pp. 416–426), Hildebrand (1982, pp. 261–263), Young (1975, pp. 210–212) and de Beer (1928, pp. 327–336).

How can one account for these phenomena? If each species had been created, why would there be this unduly complex way of making a circulatory system? Wouldn't it be simpler to begin with the adult plan? On the other hand, one could account for the data in a satisfactory manner if the concept of evolution was invoked as an explanatory hypothesis. In evolution, what is already in existence is modified. In creation, there is nothing in existence to be modified. Thus, if the early chordates had a a pattern of blood vessels as shown in

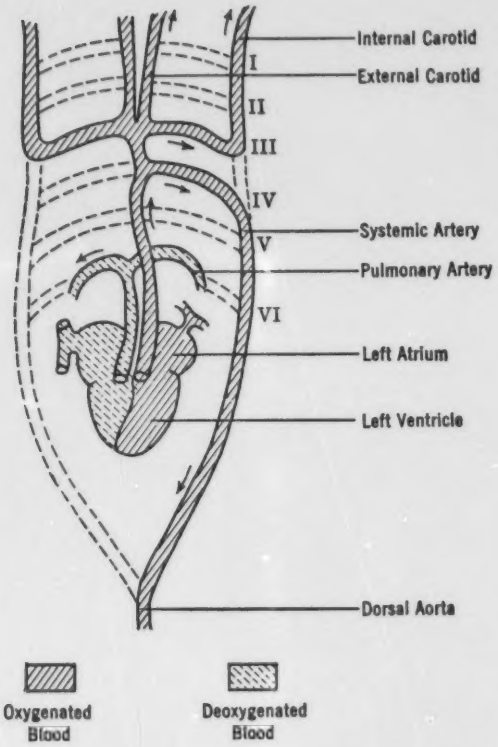

FIG. 7. The transformation of the aortic arches in a mammal.

Figure 5, modifications of that simple arrangement by retaining some of the aortic arches and eliminating others would give the very diverse patterns that characterize the different chordate classes.

There are important differences between the relation of the data on ear ossicles to the concept of evolution and the relation of the data on aortic arches to the concept of evolution. Before there was fossil evidence from the mammal-like reptiles, one could say only that the transformation of the reptilian articular and quadrate into the mammalian malleus and incus could be explained on the basis of evolution. That the concept of evolution could explain the data is *indirect evidence* for the correctness of the hypothesis. It was only later that the fossil record showed that the deduction that the reptilian articular and quadrate evolved into the mammalian malleus and incus was true beyond all reasonable doubt. The fossils, therefore, provided *direct evidence* for the correctness of the hypothesis of evolution.

In a like manner, the data on the aortic arches can be explained on the basis of the modifications of a fundamental plan to produce the conditions we observe in the classes of vertebrates. The evidence is also indirect. It seems likely that the data on aortic arches will always remain indirect evidence for the correctness of the hypothesis of evolution—hearts and blood vessels are not usually preserved in the fossil record.

Thus the concept of evolution allows us to "make sense" out of the data—and that is the grand purpose of a good theory. This is not an easy point of view to understand—especially for students—as Medawar (1981) points out:

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> The reasons that have led professionals without exception to accept the hypothesis of evolution are in the main too subtle to be grasped by laymen. The reason is that only the evolutionary hypothesis makes sense of the natural order as it is revealed by taxonomy and the animal relationships revealed by the study of comparative anatomy .... In biosystematics and comparative zoology the alternative to thinking in evolutionary terms is not to think at all.

It takes effective teaching and serious thinking by the student for this point to be mastered.

The discussion of these two examples, ear ossicles and aortic arches, emphasizes the close relationship between adult structure and embryology. This is not surprising—the structure of adults is derived directly from an earlier stage in life when they were embryos. The next deduction, therefore, will come as a natural outgrowth of the last.

Deduction 12: *If the members of a major taxonomic unit share a common ancestry, that should be reflected in their embryonic development*

Early in the 19th century embryologists noticed that embryos of different classes of chordates resemble one another much more closely that do the adults. Darwin mentioned that Agassiz had inadvertently failed to label an embryo when he first obtained it and then could not tell "whether it be that of a mammal, bird, or reptile" (*Origin*, p. 439).

After 1859 one of the main preoccupations of embryologists was to study embryos for whatever light they could throw on evolution. In those days when the fossil record was even more inadequate than it is today, the changes in the course of development were thought to reflect what had occurred in phylogeny. There could almost never be any direct evidence for the evolutionary changes in the soft tissues that fail to fossilize.

> Embryology rises greatly in interest, when we thus look at the embryo as a picture, more or less obscured, of the common parent-form of each great class of animals (*Origin*, p. 450).

As more and more vertebrate embryos were studied it seemed that, in some very general way, embryonic development did reflect evolution. This led the German biologist Ernst Haeckel (1834–1919) to propose his famous aphorism: "Ontogeny Recapitulates Phylogeny." Experience has shown that to be an extreme statement. In development we do not pass through stages in which we resemble *adult* fishes, amphibians, reptiles, and lower mammals. Nevertheless, human beings do recapitulate some of the features of the embryos of lower forms.

The basic chordate body plan. There are three diagnostic characteristics of all species that are classified as chordates: the possession of a notochord, gill slits or pouches in the pharynx, and a dorsal nerve tube. The human adult has only one—the dorsal nerve tube, which has become our brain and spinal cord. As embryos we had all three. Our notochord lasted only through the early embryonic stages. The gill pouches also disappear in development but the first becomes the Eustachian tube of our ear.

Figure 8 shows an idealized chordate with little except the three diagnostic characteristics. We now know that all chordate embryos show this same basic pattern early in development.

This discovery finds a ready interpretation if all chordates share a common ancestor. It is reasoned that the very early chordates possessed the features shown in Figure 8 and, as evolution proceeded, the embryos of higher forms continued to reflect the ancestral condition. The intense interest shown in *Amphioxus* is based on the fact that, in many aspects of its morphology, it has the features we predict for the earliest of chordates (Willey, 1894). The ammocoete larva of the lamprey is held in the same high regard—and for the same reason (Moore, 1957, ch. D-4).

The example just given resembles that of the aortic arches. The concept of evolution allows us to understand the data. And, once again, if the theory suggests an intellectually satisfying explanation and

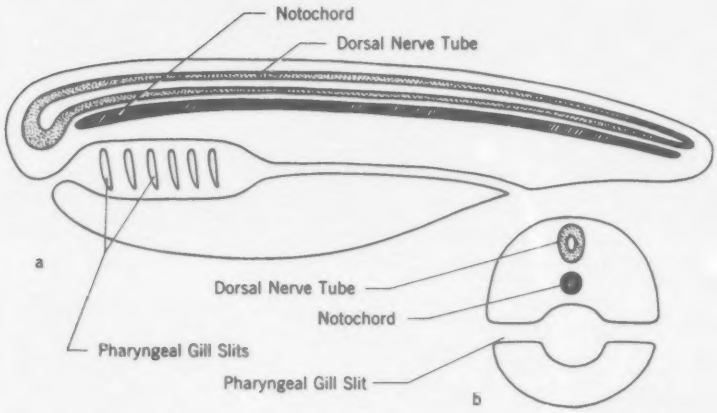

FIG. 8. An idealized chordate showing the three diagnostic characteristics: *a*. lateral view; *b*. cross section in the gill region.

does not invoke supernatural forces, it can be accepted.

The vertebrate kidneys. An even more famous case of ontogeny recapitulating phylogeny is the vertebrate kidney. Figure 9 shows the events in a highly schematic manner. The early embryos of reptiles, birds, and mammals have a kidney in the anterior portion of the coelom—the pronephros. Later in development the pronephros degenerates and a second kidney takes over—the mesonephros. It, too, disappears and is replaced by a third kidney—the metanephros, which remains as the kidney of the adult. The embryos of fishes and the agnathan lamprey start with a pronephros in the embryo and replace it with a mesonephros, which is the kidney of the adult. No metanephros develops.

Without the concept of evolution, the recapitulation of pronephros, mesonephros, and metanephros in human embryos would not make much sense. With the concept of evolution, it does.

More details are to be found in Goodrich (1930, ch. 13), de Beer (1958*b*) and Romer and Parsons (1977, ch. 13).

Deduction 13: *If evolutionary divergence is the basis of organic diversity, that should be reflected in our system of classification*

Classification, often regarded as one of the dullest parts of the biological sciences, is a device of utmost importance in enabling us to deal with everyday life. Classification consists of combining objects and ideas on the basis of some characteristics held in common. Classification is the most powerful method we possess for packaging information. It is so much a part of our lives that we forget how basic it is.

Suppose that someone begins to speak to you about a VW, one that you have never seen. Nevertheless, you automatically recognize "VW" as "automobile." With that recognition you will immediately have a vast amount of available information—about motors, wheels, seats, batteries, gasoline, role in accidents, relation to pollution and the Persian Gulf, and a host of other details.

Classification is the same information-packed and predictive device in biology. Let us suppose that you have carefully dissected and studied one mammal—fetal pig, rabbit, white rat, whatever. You are next presented with a new mammalian species, never before studied by a scientist. Without touching the creature, you would be able to make a host of predictions about its anatomy, physiology, reproduction, and development. When you checked the predictions they would be found to be correct or almost correct in most instances. To paraphrase a well-known dictum: "when you have studied one mammal, you know them all."

Different systems of classification for

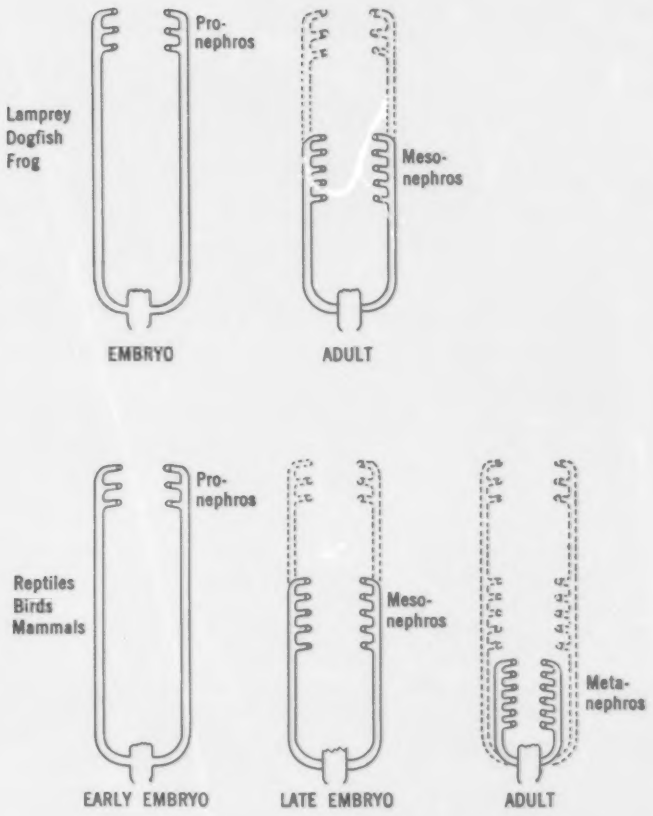

FIG. 9. Developmental changes in the kidneys of vertebrates.

biological species have been used for different purposes. The ancient Herbrews made an important distinction between animals that were clean *vs.* unclean. The clean could be eaten, the unclean not. For details see chapter 11 of Leviticus and also McKenzie (1965, pp . 141–143).

Aristotle, the father of so many fields in biology, is also acclaimed as the father of the classification of animals. The principal features that he employed were the presence or absence of blood and the mode of reproduction (Thompson, 1910). This results in the main categories shown in Table 3.

The modern period of biological classification begins with Karl von Linné (1707–1778) who regularized the system of giving Latin names to all plants and animals (including himself—"Linnaeus"; for biographies see Blunt, 1971 and Larson, 1971). His *Systema Naturae* of 1758 is the starting point for our taxonomy. Linnaeus, following Aristotle, employed a very few characteristics for classifying organisms: nature of the heart, type of reproduction, warm or cold blooded, etc. This procedure of using a only a few characteristics is called an *artificial system.*

As more and more was learned about the anatomy and embryology of animals, the artificial system proved to be inadequate: it appeared to unite species that differed in fundamental ways. It was suggested that a *natural system* of classification would better reflect the state of nature. The natural

TABLE 3. *Aristotle's basic classification of animals.*

Animals without blood	
without shells	worms
with a soft shell	crabs
with a calcareous shell	snails
with an articulate body	insects
Animals with blood	
Oviparous	
with fins	fishes
without feet	serpents
with feet	reptiles
with feet and wings	birds
Vivaparous	mammals

TABLE 4. *A typical mid 19th century classification. From Baird (1851).*

Division I. Radiata
Class 1. Infusoria (protozoans)
Class 2. Zoophyta (hydroids and sponges)
Class 3. Acalephae (medusae and ctenophores)
Class 4. Echinoderms (starfish, sea urchins)
Class 5. Intestina (flatworms, nematodes)
Division II. Mollusca
Class 1. Acephala (tunicates and bivalve mollusks)
Class 2. Gastropoda (snails)
Class 3. Pteropoda (pteropods)
Class 4. Cephalopoda (octopus, squid)
Division III. Articulata
Class 1. Annelida (annelid worms)
Class 2. Cirrhopoda (barnacles)
Class 3. Crustacea (crustaceans)
Class 4. Arachnida (spiders, mites, scorpions)
Class 5. Insecta (insects)
Division IV. Vertebrata
Class 1. Pisces (agnathans, sharks, bony fish)
Class 2. Reptilia (amphibians and reptiles)
Class 3. Aves (birds)
Class 4. Mammalia (mammals, including man)

system differed only from the artificial system in employing many more characteristics, including those of internal anatomy and development. Although the details of a natural system of classification could not be agreed upon by all, a representative one from the middle of the last century is shown in Table 4 (modified from Baird, 1851, vol. 2, pp. 213–219). The basic four divisions are those of Cuvier.

The way the natural system worked in practice can be understood by seeing how two of the "errors" of the scheme shown in Table 4 were corrected. In Division I, the Radiata, the hydroids are placed in one class and the medusae in another. That is a reasonable step if one uses only external morphology. The hydroids are plant-like species that are usually sessile. The medusae, or jellyfish, are free swimming cup or plate shaped animals—with no apparent similarities to the hydroids. Eventually it was discovered that most species of hydroids reproduce by asexual budding and the buds are medusae. Furthermore, many of the medusae reproduce sexually and the offspring are hydroids. Before this was known, there were cases where two very different forms were placed in separate classes when they were none other than parent and offspring of the same species.

A similar example is the Class Acephala of the Mollusca, which combines the tunicates and the bivalve mollusks. A bivalve mollusk without its shell is a rather amorphous creature—recall the last oyster on a half shell that you ate. The tunicates are, likewise, usually rather featureless lumps growing on wharf pilings. So bivalve mollusks and tunicates were put in the Acephala because they lacked well-marked heads and did not seem to have much in the way of positive characteristics. The story changed when the embryos of tunicates were discovered. They proved to be tiny tadpole-like larvae with a notochord, dorsal nerve tube, and pharyngeal gill slits. The adult retains only the gill slits. Thus it seemed more natural to include the tunicates with the other kinds of animals that have those three characteristics—the chordates.

One of the most vigorous supporters of the natural system was Asa Gray. He notes that the purpose of the artifical system of Linnaeus "is merely to furnish an easy mode of ascertaining the names of plants; their relationships being left out of view" (Gray, 1842, p. 185). The artificial system is still used today for one purpose—keys for identifying plants and animals. Can you consider, for example, having to check the life cycle of a putative chordate to see whether or not it ever had a notochord or pharyn-

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geal gill slits or whether a plant in hand had developed from a seed with one or two cotyledons?

The purpose of the natural system is to ascertain relationships.

> The object proposed by the natural system of botany, is to bring together into groups those plants which most nearly resemble each other, not in a single and perhaps unimportant point (as in an artificial classification), but in all essential particulars; and to combine the subordinate groups into larger natural assemblages, and these into still more comprehensive divisions, so as to embrace the whole vegetable kingdom in a methodical arrangement. All the characters which plants present, that is, all the points of agreement or difference, are employed in their classification; those which are common to the greatest number of plants being used for the primary grand divisions; those less comprehensive for subordinate groups &c.; so that the *character*, or description of each group, when fully given, actually expresses all the known particulars in which the plants it embraces agree among themselves, and differ from other groups of the same rank. This complete analysis being carried through the system, from the primary divisions down to the species, it is evident that the study of a single plant of each group will give a correct (as far as it goes), and often a sufficient idea of the structure, habits, and even the sensible properties of the whole (Gray, 1842, p. 191).

But what can possibly be the basis of there being groups of related species? We noted before that if species are separately created they cannot be related in any biological manner whatsoever. Yet there are groups of organisms: groups of individuals make up a species; related species are united in a genus; related genera in a family; related families in orders, orders in classes, and so on.

It was difficult to provide a naturalistic explanation for how there could be natural groups. Some saw no need to. Agassiz recognized the problem and offered a personal answer.

> The divisions of animals according to branch, class, order, family, genus, and species . . . constitute the primary questions respecting any system of Zoology, [and] seem to me to deserve the consideration of all thoughtful minds . . . . To me it appears indisputable, that this order and arrangement . . . [are] in truth but translations into human language of the thoughts of the Creator (Agassiz, 1859, pp. 8–9).

By 1859 the major groups had been delimited in a manner that, for the most part, are the natural groups we recognize today. This had been accomplished by detailed studies of the anatomy of the adults and the beginnings of information on development. When the hypothesis of evolution was suggested there was no change in the system of classification. What had changed was, for the first time, there was a naturalistic explanation for how there could be natural groups: the data could be explained by the hypothesis that all the members of any taxonomic group—from species to phyla—shared a common ancestor.

The deduction has proved to be true.

Deduction 14: *If there is a unity of life based on descent from a common ancestor, this should be reflected in the structure of cells*

And it is—to an astonishing degree. Common ancestry demands a unity of life and nowhere is this more obvious than in the fact that the bodies of nearly all organisms are built of the same units of structure—cells.

By the time of the *Origin* it was becoming increasingly obvious that cells are important structural units in plants and animals. Plant cells, or more properly their walls, had been known for generations and often illustrated beautifully (Grew, 1682; Moore, 1972*b*, pp. 28–35). In 1839 Theodor Schwann had made a cogent case for cells being a fundamental unit of structure in animals (see Moore, 1972*a*, ch. 2) but to him cells were not permanent structures;

they were formed by the body in a process thought to resemble crystalization. In 1855 Virchow suggested the hypothesis *omnis cellula e cellula* (all cells from cells) which, when proved to be true, suggested that every cell is the current expression of a lineage of life extending back in time to the origin of life itself.

During the last half of the 19th century, considerable knowledge of cells at the level of resolution of the light microscope was obtained. Cells were found to exist in great variety but all shared a basic structure consisting of an outer limiting membrane, a nucleus, and associated cytoplasm. *Omnis cellula e cellula* was accomplished by mitosis except in the formation of gametes—then meiosis was the mechanism. There were questions about the microorganisms—were bacteria really cells and did they have a nucleus? These debates lasted until the availability of the electron microscope (EM) and improved techniques settled many issues of fine structure.

For us today the most exciting information about cell structure is coming from EM studies. This new knowledge has even resulted in a fundamentally different scheme of classification. The old system, up to about 1950, recognized three main kingdoms: microorganisms, plants, and animals. Today more and more biologists prefer a scheme that recognizes five kingdoms, with a fundamental distinction between organisms with nucleated cells and those with non-nucleated cells (Whittaker and Margulis, 1978; Luria, Gould, and Singer, 1981, pp. 754–757). Those without nuclei are known as Prokaryota ("before nucleus") and those with nuclei as Eukaryota ("true nucleus"). This is the scheme:

Prokaryota
- Kingdom 1. Monera: bacteria, mycoplasms, spirochaetes, blue-green algae.

Eukaryota
- Kingdom 2. Protista: protozoans, green algae.
- Kingdom 3. Fungi: yeasts, molds, mushrooms.
- Kingdom 4. Animalia: multicellular animals.
- Kingdom 5. Plantae: red and brown algae, bryophytes, vascular plants.

Evolutionists in the 19th century more or less accepted the hypothesis that life must have started with organisms at least as simple as a bacterium yet few of them would have dared to be so optimistic as to believe that a useful fossil record existed for such tiny and fragile creatures.

In recent years, however, new methods of collecting and preparing specimens are providing us with information about organisms that lived more than three billion years ago. The oldest so far discovered are from Western Australia and South Africa. The Australian material comes from a site with the improbable name North Pole (Groves, Dunlop, and Buick, 1981). There, in the Warrawoona Group rocks, specimens identified as blue-green algae with a probable age of 3.5 billion years have been discovered. The Fig Tree Chert of South Africa has yielded what seem to be bacteria (*Eobacterium*) and blue-green algae (*Archaeospheroides*). Thus the first evidences of life are of prokaryotes that are much like the prokaryotes living today.

Living prokaryotes are all small—usually less than 10 micrometers and some only 0.2 micrometers. In common with all cells, there is an outer limiting membrane or plasmalemma. The contents of the cell are not compartmentalized. There are ribosomes but no mitochondria, Golgi, chloroplasts, or lysosomes. There is no nucleus, that is, a membrane-bound vesicle containing chromosomes. There is, of course, DNA. This is in the form of a double helix, which is not associated with proteins, and is free in the cell. The DNA may form a tangled mass visible with the EM as a nucleoid.

The characteristic features of the prokaryotic cell, therefore, are a plasmalemma, RNA-containing ribosomes, and naked DNA. We are now realizing that this

was the limit of evolutionary complexity for most of life's span on earth. The generally accepted date for the formation of the earth is 4.5 billion years ago. The oldest known prokaryotic organisms date to 3.5 billion years ago. There is considerable debate about the earliest eukaryotic organisms—paleocytology is a difficult field—but a date of 1 billion years ago seems the best we can do for the present. Thus for the first 70 percent of the time life is known to have existed, only prokaryotic organisms were present. This level of organization permitted only tiny cells that existed singly or formed simple filaments. But masses of filaments can form large structures. For example, the stromatolites that occur on some coasts may form large biscuit shaped structures. Fossil stromatolites, dating back about 1.8 billion years, are known from the Great Slave Lake region of Canada and about 3.5 billion years ago from Western Australia (Walter, Buick, and Dunlop, 1980). Nevertheless, no prokaryotic cells show the complexity of eukaryotic cells and they have not been able to form complex multicellular organisms with many kinds of differentiated cells.

Then about a billion years ago, life took a momentous step—the eukaryotic cell came into existence. The important difference between a prokaryotic and eukaryotic cell is that the latter has some of its contents compartmentalized. That is, related sets of molecules concerned with the same function are surrounded by membranes that provide some isolation and regulate the passage of materials in and out of the compartments. The DNA, now associated with protein, is surrounded by a nuclear membrane with pores. The energy-yielding reactions are compartmentalized in mitochondria. The photosynthetic reactions of green plants are isolated in chloroplasts. Some of the secretory processes are restricted to the Golgi. Other membrane systems, such as the endoplasmic reticulum and the associated ribosomes, provide the protein synthesizing machinery of the cell.

In recent years an interesting hypothesis for the origin of certain organelles of eukaryotic cells has gained increasing support. The suggestion is that structures such as mitochondria and chloroplasts began as prokaryotic cells. These entered other cells where they became symbionts. The result was the eukaryotic cell. Margulis (1981) provides a summary of the evidence. Examples of symbiosis have long been known: algae and fungi cooperate to form lichens; algae live in the cells of several kinds of animals, including the giant clam, to which they supply food; and the nematocysts of coelenterates survive digestion by nudibranchs and are moved to the nudibranch's dorsal surface where they function in defense of the host.

Once the functions of cells became compartmentalized, as at the eukaryotic level of organization, there can be a true division of labor. With time this permitted the evolution of multicellular organisms with some cells different from others. Groups of specialized cells then took over the separate physiological functions. Yet even in the largest and most complex organisms the fundamental unit of structure and function remains the cell. The cells of eukaryotic organisms form an integrated whole. The functioning of the individual cells of the complex eukaryotic organisms can be seen as necessary for the life of the organism just as the functioning of the organism seems to be concerned mainly with the life of its individual cells. The cell is the organism's way of doing things just as the organism is the cell's way of doing things.

Most of the details of structure and function in the cells make sense because what cells are and what they do are reflections of their evolutionary history.

Some useful references to this rapidly changing field are Bernal (1967), Margulis (1970*a*, 1970*b*), Orgel (1973), Ponnamperuma (1972), Knoll and Barghoorn (1977), Hanson (1977), Dickerson (1978), J. W. Schopf (1978), Woese (1981), Cloud (1978), Folsome (1979), Scientific American (1979*a*), Walter, Buick, and Dunlop (1980), Groves, Dunlop, and Buick (1981), Barghoorn (1971), Cloud and Glaessner (1982), Avers (1976), and Freifelder (1983).

Deduction 15: *If there is a unity of life based on evolution, that should be reflected in the molecular processes of organisms.*

There is a tremendous diversity in structure, physiology, and behavior among the species of the five kingdoms of life. There is far less diversity in the cells of which their bodies are composed. There is still less diversity in the basic molecular processes that occur in all cells. This has become clear only in recent years with the wealth of new techniques available for the study of molecular events in cells.

The fact that the basic metabolic reactions in the cells of all organisms are so much alike can be interpreted to mean that they developed in the first stages of life and have been retained, with relatively little modification, in the descendants. It is difficult to find another naturalistic explanation. We cannot study the molecular reactions of those ancient blue-green algae and bacteria from the North Pole deposits of Australia or the Fig Tree Cherts of South Africa. Nevertheless, these ancient progenitors have closely similar living counterparts and, by studying them, we can make reasonable inferences about what happened in the past.

Some of the more striking of these molecular uniformities are:

1. All cells consist of the same classes of organic compounds: nucleotides, proteins, lipids, and carbohydrates.

2. Reactions involving these organic compounds are controlled in all cells by the same class of proteins—the enzymes.

3. In all cells, DNA contains the coded information that regulates the life of the cell and transmits the information to the next generation. (In a few types of viruses the closely similar RNA performs the same functions.)

4. In all organisms, DNA is composed almost entirely of combinations of six kinds of molecules: 2 pyrimidines (thymine and cytosine), 2 purines (adenine and guanine), a sugar (deoxyribose), and phosphate. The purine and pyrimidine bases are sometimes chemically modified.

5. In all organisms, RNA is composed of combinations of six kinds of molecules: 2 pyrimidines (uracil and cytosine), 2 purines (adenine and guanine), a sugar (ribose), and phosphate. Again, the bases are sometimes chemically modified.

6. The DNA code, which transmits hereditary information from generation to generation, and provides the information for intracellular synthesis and control, consists of the sequence in which the purines and pyrimidine bases are arranged. Each specific triplet of bases is related to a specific amino acid. The code is universal for all forms of life—a simply astonishing fact, except within the context of evolution.

7. In all organisms the specific information encoded in DNA serves as a template for the synthesis of specific messenger RNA. Enzymes organized by specific messenger RNA molecules, in cooperation with transfer RNA, join amino acids to form specific proteins.

8. In all cells, proteins are synthesized from about 20 kinds of amino acids. Except for the 5 carbon sugars of DNA, RNA, ATP and other specialized molecules including some co-enzymes, the major carbohydrates of cells consist of 6 carbon sugars, such as glucose, and polymers of 6 carbon sugars, such as starch and cellulose. Important lipids in all cells consist of glycerol plus 3 molecules of fatty acids or 2 molecules of fatty acid and 1 molecule of a phosphorus-containing compound. Nucleic acids, proteins, carbohydrates, and lipids account for nearly all of the organic compounds of life, of which there are enormous numbers of kinds. Nevertheless, this great diversity is based on relatively few building blocks—much as the rich English language combines only a few of the 26 letters to fill an unabridged dictionary.

9. All cells obtain energy by oxidizing reduced compounds, as in glycolysis—the anaerobic fermentation of glucose to pyruvic acid. In glycolysis, chemical energy is transferred to convert ADP to ATP. ATP is the immediate energy source for cells. Some prokaryotes and most eukaryotes use oxygen as a major electron acceptor, as in the aerobic breakdown of pyruvic acid to carbon dioxide and water. In these aerobic

E8 90

processes, as compared with anaerobic reactions, much more energy is transferred to convert ADP to ATP. These are striking examples of the fact that many of the basic metabolic pathways are the same or similar in all cells.

Most of the energy for life is the energy of sunlight captured by green plants in the reactions of photosynthesis and stored in carbohydrates. Chemosynthetic bacteria carry out processes very similar to those of other organisms, even though they power their reactions from reduced compounds such as methane, rather than from sunlight.

10. Nowhere is the biochemical unity of life shown more dramatically than in experiments where genes of higher organisms, such as human beings, can be incorporated into the DNA of bacteria. There, using the bacterial synthetic machinery, the human gene can direct a human-type protein to be synthesized.

Although the sorts of data just listed are not proof of evolution, there is no other naturalistic explanation that can make as much sense of them. Similarly, there are no molecular data that falsify the concept of evolution. More than anything else, the molecular data point to a unity of life based on common descent.

Many more examples of the biochemical unity of life could be given and there is an almost irresistable urge to do so—mainly because so much of it is recent and hence of great interest to us (the teachers). Students may be content with a more modest dose, especially if it means that they will be introduced to other equally important ideas—new to them but old for us.

For more details see Purves and Orians (1983), Dustin (1980), Avers (1976), Luria, Gould, and Singer (1981), Dickerson (1972, 1978), Folsome (1979), Margulis (1970*b*), Orgel (1973), Ayala (1976), J. W. Schopf (1978), Scientific American (1979*a*), Nei and Koehn (1983), and Freifelder (1983).

A summing up

This ends our formal analysis of Darwinism, which was accomplished mainly in a series of deductions stemming from the proposition, "If the hypothesis of evolution is true . . . ." The first 10 deductions sought a direct test of the hypothesis. The last 5 emphasized the role of the hypothesis in bringing rational order to the data of biology and geology.

It is this second function of the concept of evolution that has so impressed scientists. To a considerable degree the two statements quoted earlier—Dobzhansky's that "Nothing in biology makes sense except in the light of evolution" and Medewar's that "the alternative to thinking in evolutionary terms is not to think at all"—are fully accepted by scientists familiar with the data of biology and geology.

In the last half of the 19 century the concept of evolution guided the research programs in comparative anatomy, cytology, inheritance, paleontology and, to a lesser degree, in systematics and animal behavior.

By 1900 Darwin and other scientists had made it possible to accept as true beyond all reasonable doubt that evolution had occurred. The most direct evidence had come from paleontology but all major disciplines of biology made a contribution. The more original portion of Darwin's thesis, namely that the mechanism of evolutionary change is primarily natural selection acting on variations, was not generally accepted. Fleeming Jenkin continued to be the monkey on Darwin's back—and would remain so until routed by Mendelian genetics.

Evolution after Darwin

The last edition of the *Origin* was published in 1872 and Darwin was interred in Westminister Abbey April 26, 1882 a few feet from another of England's illustrious sons—Sir Isaac Newton. Together they had revolutionized the biological and physical sciences.

The amount of research performed in the last hundred years that relates directly or indirectly to evolutionary biology is enormous in quantity but more modest in conceptual advances. For the most part the work has been "normal science" as Kuhn (1970) designates the mopping-up activities that follow a scientific revolution.

The problem for those teaching first-year

college and university courses in general biology is to select among the many topics that might be considered a few that can be given meaningful consideration in the ever tight schedule. My suggestions will follow. They tend to be those topics that have been well documented and are of obvious importance to evolutionary theory. Some of the more active fields in evolutionary biology today do not meet these two criteria and I cannot see that they should be included to the exclusion of the other suggested topics. I prefer to include what is important and probable in a first-year course and leave the more questionable areas of research to advanced courses.

After a period of intense activity and interest in the years following the *Origin*, evolutionary biology underwent an eclipse. Then, in the 1930s, there was renewed activity that saw the then isolated fields of genetics, systematics, and paleontology addressing in unison the problems of evolution. This was the "Modern Synthesis" that set the course for research and speculation that lasts to this day (Mayr and Provine, 1980).

The seminal works of the Modern Synthesis were Dobzhansky (1937), Mayr (1942), and Simpson (1944), to which we should add Fisher (1930), Wright (1931), and Haldane (1932) who provided a mathematical framework for the analysis of natural populations and evolutionary change. Most of these founding fathers revised their initial contributions: Dobzhansky (1970), Mayr (1963, 1970), Simpson (1953), and Wright (1968–1978).

Other useful sources of information and analysis, appearing in this century but mainly since the Modern Synthesis, are: Headley (1900), Morgan (1903), Weismann (1904), Lock (1906), Butler (1911), Crampton (1911), Geddes and Thomson (1911), Dendy (1912), Delage and Goldsmith (1913), Lloyd (1914), Morgan (1916), Lull (1917), Morgan (1925), Kerr (1926), Morgan (1935), Robson and Richards (1936), de Beer (1938), Goldschmidt (1940), Cott (1940), J. Huxley (1940, 1942), Lack (1947), Clausen, Keck, and Hiesey (1948), Jepsen, Mayr, and Simpson (1949), Simpson (1949), Schmalhausen (1949), Stebbins (1950), Simpson (1953), J. Huxley, Hardy, and Ford (1954), Dobzhansky (1955), Mayr (1957), Maynard Smith (1958), Rensch (1959), Tax (1960), Blair (1961), Dobzhansky (1962), Rhodes (1962), Grant (1963), Mayr (1963), G. C. Williams (1966), Jukes (1966), Dobzhansky, Hecht, and Steere (1967–), Wright (1968–1978), Ehrlich, Holm, and Raven (1969), Mayr (1970), Grant (1971), Dobzhansky (1970), Salthe (1972), Ehrlich, Holm, and Parnell (1974), Lewontin (1974), Nei (1975), Frazzetta (1975), Mayr (1976), Ayala (1976), Stebbins (1977), Volpe (1977), Grant (1977), Dobzhansky, Ayala, and Valentine (1977), M. J. D. White (1978), Futuyma (1979), Solbrig and Solbrig (1979), Ayala and Valentine (1979), Stanley (1979), P. J. Darlington (1980), Mayr and Provine (1980), B. Wallace (1981), Atchley and Woodruff (1981), Mayr (1982), Maynard Smith (1982), Stebbins (1982), Milkman (1982), and Ayala (1982). These references are in chronological order to enable one to trace the evolution of our thinking about evolution—there was a great change in what was said after the Modern Synthesis of the 1930s and 1940s.

The fossil record

Today very much more can be said about the history of life than was possible in Darwin's time. Generations of paleontologists have explored most of the earth's crust and filled the museums with fossils. The data of paleontology that were supportive of the concept of evolution a century ago have now reached the state where all with an open mind will regard them as complete proof. Nevertheless there is much more to be learned. As is true with all science, each discovery provides more questions than answers.

Darwin spoke of "the imperfection of the geological record." It is still imperfect but this is a consequence of the fact that we are asking more difficult questions. In Darwin's day the principal information desired was whether or not organisms intermediate between major groups had ever existed as the hypothesis of evolution demanded. *Archaeopteryx*, the fossil, said "yes." But once that question was answered it was only natural that scientists would wish

to know about links between the archosaurian reptiles and *Archaeopteryx* and between *Archaeopteryx* and more modern birds. Thus for each missing link discovered there were two missing links to be sought.

The ultimate goal of paleontology is to document, to the greatest extent possible, the lineages of life. This has been accomplished but only in a very elementary manner—even for the chordates, which provide us with the best data. For some of the very important questions, for example the antecedents of the phyla, there is almost no solid information (House, 1979).

One problem relating to the interpretation of the data should be mentioned. Some paleontologists are reluctant, and wisely so, to say whether or not a specific fossil is on the *direct* ancestral line to a later fossil species or to a surviving species. To offer such an opinion with any high degree of confidence would require a huge sample of fossils from rocks of slightly differing ages covering the entire span from the putative ancestor to the putative descendant. Such a complete record has never been available but, for the basic question, it is not essential. What is required is fossils that are intermediate in structure and occurring in strata of intermediate age.

These are some of the important points, in my opinion, that are appropriate to discuss with first-year students.

1. Does the fossil record, broadly considered, present a consistent pattern? That is, do the fossils of successive strata show trends or is their distribution in time random? Do the prokaryotes appear first and the more complex forms in some reasonable sequence? The answer to all of these questions is "yes." One does not find jaw bones of apes and leg bones of horses in the oldest known rocks. There is a sequence that makes sense—as was already known to Buckland (1836) and Lyell (1826) (Table 2). The work of the last century has made this conclusion even more certain. Any good modern textbook of geology such as Raup and Stanley (1978), Dott and Batten (1976), and Seyfert and Serkin (1979) may be consulted for details.

2. Is there good evidence for intraphylum evolution among the chordates? Yes, rather good and getting better. The broad picture can be extracted from Colbert (1980), Romer (1966), and Romer and Parsons (1977, ch. 2). The following is a synopsis of the main lineage from the earliest chordates to human beings.

The earliest known chordate is the agnathan, *Anatolepsis*, from the Upper Cambrian of Wyoming. The first jawed fishes, the acanthodians, date from the Silurian and were followed by an extensive radiation of fishes in the Paleozoic. Crossopterygian fishes such as *Eusthenopteron*, which were ancestral to the amphibians, appear in the Devonian. *Ichthyostega* of the Upper Devonian is clearly intermediate between crossopterygian fishes and labyrinthodont amphibians.

The amphibians radiated extensively in the Paleozoic. In the late Carboniferous the labyrinthodont amphibians gave rise to primitive reptiles and again the fossil data are convincing. One genus, *Seymouria*, is such a blend of amphibian and reptilian features that it is arbitrary whether it should be classed as one or the other. The earliest reptiles, the cotylosaurs, date from the Carboniferous. All other reptiles evolved from them, including the late Carboniferous synapsids, which are on the line to mammals. In the Permian the theriodont reptiles, such as *Cynognathus*, show some of the morphological features characteristic of the primitive mammals. The first mammals appear in the Triassic. The transition from mammal-like reptile to mammal has been especially well documented. In addition to Colbert (1980) and Romer (1966), see Sloan (1983), Kemp (1982), and Broom (1932).

Earlier this year an exciting new intermediate type was discovered. The cetaceans—whales, porpoises, and dolphins—were already known to occur in the early Cenozoic by which time they were fully formed for aquatic life. Their origin was a mystery but on anatomical grounds their ancestors were suspected. Colbert (1980, p. 326) made this prediction:

> Cetaceans are certainly the most atypi-

> cal, and in many ways the most highly specialized [mammals] in the extent to which they have diverged from their primitive eutherian ancestors. [They] probably arose in early Cenozoic times from primitive carnivore-like ungulates known as mesonychids.

That may appear as a bold, though improbable, prediction since the carnivores are dog-like and the ungulates include horses and related species. Whales might not appear to have much resemblance to either. But Colbert was correct. Gingerich, Wells, Russell, and Shah (1983) and Gingerich (1983) have reported the discovery of *Pakicetus* in early Eocene strata in Pakistan. It is intermediate in structure between the mesonychid land mammals and the middle Eocene whales. The authors conclude: "Evidence suggests that *Pakicetus* and other early Eocene cetaceans represent an amphibious stage in the gradual evolutionary transition of primitive whales from land to sea."

This discovery is important for adding another bit of information about the evolutionary radiation of the mammals. It is of even greater importance for students in showing the accuracy of predictions in evolutionary biology. Not only was a predicted intermediate type discovered but it was found in strata of the predicted age. The geological record may be inadequate in providing a detailed account of the radiation of mammals yet it is complete enough so that new discoveries provide few real surprises. Had *Pakicetus* never been discovered, already existing evidence would have made it highly likely that the cetaceans had evolved from the mesonychid land mammals and done so in the early Cenozoic. QED.

3. Does the fossil record provide more detailed lineages? Not very many, but there are notable examples. Some of the better are of invertebrate groups, which tend not to be so meaningful to students. One of the best among the vertebrates is still the venerable story of horse evolution. In addition to Colbert (1980) and Romer (1966), see Simpson (1961), Woodburne (1982) and MacFadden (1977, especially for the reproduction of Huxley's delightful drawing of "Eohippus + Eohomo"). See Gingerich (1983) for other examples.

As an interesting sidelight, the American West proved to be a rich source of fossil vertebrates and the discoveries were of worldwide importance in the last part of the 19th century. The United States government supported four major expeditions to the West: those of King, Hayden, Wheeler, and Powell (Stegner, 1954; Bartlett, 1962; Goetzmann, 1966). Two of the more important paleontologists who worked the West were Cope and Marsh. Their colorful relationship is described in the three references just given plus Osborn (1931), Schuchert and LeVene (1940), and Ostrom and McIntosh (1966).

4. What is the rate of evolution? Simpson (1944, ch. 1 and 1953, chs. 1–2) and T. J. M. Schopf (1982) provide estimates.

Most living species of mammals go back 100,000 years, Almost none go back 1,000,000 years. The mean may be about 200,000 years between the appearance of one species and the next.

The evolution of different genera in horses required about 5.5 million years. About 20 million years were required for genera of ammonites. Some genera seem to last forever—the brachiopod genus, *Lingula*, has spanned 400 million years.

Evolution is, as Darwin suspected, a very slow process.

5. Can geological time be measured accurately? There are now numerous independent radiometric methods for measuring the time when rocks were formed—and hence the age of fossils within them. The most important fact to be noted is that different methods give the same answers. This ability to confirm was never possible with earlier methods, such as salt in the ocean, that later proved to be inaccurate. There have been many reviews: Eicher (1976), Brush (1982), Harland *et al.* (1983), Hurley (1959), and Berry (1968).

6. What can be said about the origin of life? A great deal has been said but this reflects the degree of interest in the question more than the amount of information

available. The data that can be accepted are that the geologically oldest organisms are similar to the simplest organisms known today—bacteria and blue-green algae—and that it is possible to simulate what are thought to be the chemical and physical conditions of the early earth and observe the spontaneous formation of some of the key molecules that characterize life.

Oparin (1938, 1968) and Haldane (1929) proposed the hypothesis that is generally accepted today as a working model. There was a prebiotic chemical evolution that resulted in the oceans containing a large variety of organic molecules—the thin hot soup stage. Other possibilities have been suggested such as the origin of life in association with the sort of conditions now being observed near the hot steam vents of the ocean floor. Eventually, and with great improbability, a molecule capable of self-replication, such as a nucleic acid, was formed. There must have followed an assemblage of molecules that could promote the self-replication of nucleic acid—perhaps in microspheres as Sidney Fox (1965, 1981) suggests. Then in some wholly unknown manner the cellular level of organization was reached. To this day cells remain the fundamental units of structure and function. Except for *in vitro* laboratory experiments, it takes the biochemical machinery of a cell to synthesize new DNA—and only a cell can produce another cell.

In 1863 Darwin wrote "It is mere rubbish, thinking at present of the origin of life" (F. Darwin, 1888, vol. 3, p. 18). We can do much better a century later but still we have no more than some probabilities and some possibilities to test and contemplate. The important point today is that the problem is approachable. See Bernal (1967), Ponnamperuma (1972), Scientific American (1979*a*), Folsome (1979), Fox (1965, 1981), Margulis (1970*a*), Dickerson (1978), Eigen *et al.* (1981), Nei and Koehn (1983), and the other references given earlier when cells and biochemical similarities were discussed.

The genetic basis of evolution

The lack of reliable information about inheritance prevented careful thinkers from accepting Darwin's explanation for the *mechanisms* of evolution. Darwin could neither account for the origins of new variations nor their persistence. He assumed that the environment, or conditions of life, must somehow be associated with the origin of variation. Darwin was reluctant to accept the Lamarckian view that the environment induces specific variations. Somehow new variations must arise by chance. But once they had appeared, he could not counter Fleeming Jenkin's argument that they would be quickly diluted in blended inheritance.

The rapid increase in our understanding of the mechanisms of inheritance after 1900, when Mendel's work became generally available, put evolutionary theory on a sounder basis. The essential points to be emphasized in a first-year course should include these:

1. The variation that is of importance in evolution is a consequence of the action of genes.

2. There is no blending of genes in inheritance. In heterozygous cells the different alleles are not modified by their association. Their reappearance in subsequent generations, in unmodified form, demonstrates this basic fact. The old notion of blended inheritance was based on perfectly valid observations: if two quite different individuals are crossed, their offspring are usually more or less intermediate. It was only when Mendel and his followers concentrated on individual characters, not the sum total of all characters, that it became obvious that blending does not occur.

3. New variations arise by changes in DNA: mutations at various loci, changes in chromosome structure, etc.

4. Although the rate of mutation is very low for any one locus, given the very large number of loci, new variations are appearing constantly. Although the individuals of most species resemble one another very closely, there is nevertheless a huge amount of hidden genetic variability. It has been estimated that as many as a third of all loci may be polymorphic.

5. This huge amount of heterozygosity means that crossing over in meiosis will result in an even greater variety of genetically different gametes.

6. Thus mutation plus genetic recombination result in highly diverse offspring. It has been suggested, for example, that every human being (apart from identical twins) has a unique genetic endowment that probably never existed before or will recur in the human population. There is ample variation on which natural selection can act.

7. Mutation consists of changes in the structure of DNA. In many instances this appears to be a consequence of an error during the replication of DNA or defects in the DNA repair mechanisms. The replication and repair systems can be adversely affected by some radiations, chemicals, temperature, etc. and, thus, they increase the frequency of mutations.

8. To the best of our knowledge mutation is random with respect to the locus involved and in the specific alteration of DNA structure that occurs. The neo-Lamarckian view that the type of mutation is directly related to the environmental stimulus is without foundation. The neo-Darwinian view that mutation is random and that natural selection is responsible for selecting some mutants and eliminating others accords with available data.

9. In the absence of selection the allelic frequencies remain the same as described by the Hardy-Weinberg population formula where, given alleles p and q, their equilibrium frequencies will be $p^2 + 2pq + q^2 = 1$. Thus evolution will occur when conditions alter the Hardy-Weinberg equilibrium and change the frequencies of genes.

Changing gene frequencies

Evolution is a sustained and appreciable change in gene frequencies in a population. These changes can be the result of natural selection, genetic drift, or both.

Natural selection, assumed be an ubiquitous force in evolution, has not been easy to demonstrate. There are, however, many situations where it seems highly probable that existing differences among populations are the consequences of natural selection.

Since Darwin's day it has become obvious why selection is difficult to observe, as we have noted earlier. Any natural population will have been subjected to natural selection throughout its history. At any one time the genetics of the population will be the best that mutation and natural selection have accomplished, not what *might* be accomplished had selection been more rigorous. The likelihood is remote for an investigator being able to observe a population at a time when there are significant genetic differences between the individuals that survive and those that do not.

On the other hand, if a population faces a new environmental challenge—one for which it has not been selected in the immediate past—there is the possibility of an observer documenting changes in gene frequencies. This has proved possible in three sorts of situations: industrial melanism in moths and the development of resistance to pesticides in arthropods and to drugs in microorganisms.

The peppered moth (*Biston betularia*) of England and many other species of moths living in the more heavily industrialized regions of the world have evolved melanic forms in the years since the Industrial Revolution. This can be documented in many cases because naturalists have collected moths for many years and deposited the specimens in museums. Therefore the recent history of the population is known. The genetics of melanism can be determined by crossing the original and the melanic forms.

This problem has been worked out beautifully by Kettlewell (1959, 1973). In non-industrialized regions of England the tree trunks have heavy growths of pale-colored lichens. The moths in such places are also pale. In industrialized regions gases kill the lichens and expose the dark tree trunks. In the last century melanic forms of the moths have become common in these areas. Mutations to the melanic form seem to occur throughout the range of the species. If they happen to appear in the non-polluted areas, they are conspicuous on the pale trunks and thus more easily seen and captured by birds. If they appear in an industrial area, they will be protectively colored and have a better chance of surviving. Laborious field observations have shown that this actually occurs. Natural selection, in this case predation by birds,

causes notable changes in the frequencies of the alleles that control the moth's pigmentation.

It may be necessary to emphasize to students that this is *not* an example of Lamarckian evolution—common sense might suggest that the polluted environment is somehow directly causing the change in pigmentation. The data seem conclusive that melanic mutations occur at random throughout the range of *Biston*. The polluted environment is not the cause of the mutation to melanism but if such a change occurs it will be favored by natural selection.

A very large number of insects and other arthropods have become resistant to pesticides. Many kinds of microorganisms have become resistant to antibiotics and other drugs. In those cases that have been carefully analyzed, the explanation is the same as for industrial melanism. Mutations appear by chance. If they happen to increase the survival of the individuals in their new environment—one with pesticides or drugs—they increase in frequency.

Brown (1971), Georghiou (1972), and Georghiou and Taylor (1976) have provided reviews of selection by pesticides and Richardson (1978) for the evolution of resistance to biological control. For microorganisms see Elliott (1973). All of the recent books on evolutionary biology provide general discussions of natural selection.

Genetic drift. An accidental change in gene frequencies can occur when a few individuals of a population become isolated from the rest. The few indivuduals will have only a sampling of the alleles of the entire population so any new population that develops from these "founders," as Mayr calls them, will differ from the original population.

It may be unwise to discuss genetic drift in a first-year course. There is so much that might be discussed that a selection of topics is a necessity. Genetic drift has interested evolutionists for decades but its importance relative to natural selection is probably slight. In any event it is but part of the more general phenomenon of genetic change. Once a portion of a population becomes isolated from the bulk of the population, or a population is greatly reduced in size and so comes to have a different gene pool, it will continue to be molded by natural selection. Natural selection is continuous; genetic drift is rare and episodic.

Patterns of evolution

Given the reality of inherited variability in populations and the efficacy of natural selection, one can by logical induction predict the slow change of a population over time. Thus one can begin some three billion years ago with an ancient prokaryote population and understand how we became its descendants. Here we have the evolution of a single lineage and, at any one time, only a single species of that lineage is present.

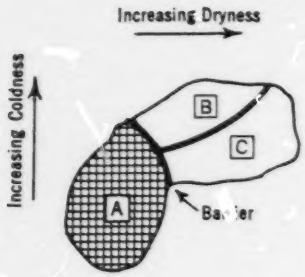
The interaction of variation and natural selection alone, however, cannot explain the presence of the millions of species on the earth today or the vastly greater numbers that occurred throughout the past. That was Darwin's main problem—what is the origin of species?

Darwin and the naturalists who followed him were much impressed with the frequent difficulty in deciding whether two populations should be considered a single species or two. The two populations might run the gamut from seeming identity, to differing in slight ways, to differing enough to be regarded as subspecies, or to being so different that they could be considered specifically distinct. The answer was clear to Darwin—the gamut reflected different degrees of evolutionary divergence.

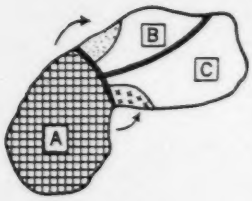
It was noted frequently that the extent of the differentiation was associated with barriers to dispersal: two subpopulations might be separated by a mountain range or other condition inhospitable to the organisms. This seemed to be a clue. It was not possible to understand how a single population in which all individuals had the opportunity to interbreed freely could split into two species, *i.e.* speciate. On the other hand if the population was physically divided by some barrier to free dispersal, one could imagine how the isolated subpopulations might slowly evolve differences from one another.

The evidence now seems overwhelming

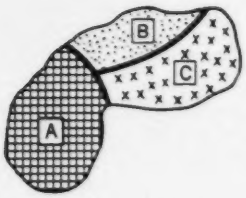
GEOGRAPHIC SPECIATION



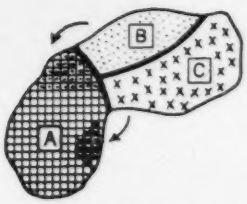
Time 1. Single Species.
The population is restricted to Zone A.



Time 2. Single Species.
Some individuals have migrated to Zone B and others to Zone C. Selection will promote the development of a population adapted to a cold, dry environment in B and to a warm, dry environment in C.



Time 3. Three Subspecies.
Evolution through the selection of spontaneous mutations in the three isolated populations has reached the point where each zone has its own adapted population. These populations, though slightly different from one another, could still interchange genes, consequently they are subspecies.



Time 4. Three Species.
The three isolated populations have diverged to the point where isolating mechanisms prevent the interchange of genes. If individuals from either Zone B or Zone C migrate back to Zone A, they can occupy this zone together with the Zone A species without the danger of losing their specific identity.

FIG. 10. A model for geographic speciation.

that this pattern, *geographic speciation*, is the principal mechanism for the origin of new species. Figure 10 shows the events in highly schematic form.

The importance of geographic speciation in evolution had long been recognized by naturalists but it was largely due to Mayr's book in 1942 that this information came to the attention of geneticists. That interdisciplinary communication was one of the more notable events in the "Modern Synthesis" of evolutionary thought. For

more recent discussions of geographic speciation see Mayr (1963, 1970, and 1982, pp. 411–417).

Chromosomal changes and speciation. Not infrequently students ask whether or not scientists have ever observed the origin of a new species. The answer is "no" for geographic speciation—the time required is in the thousands of years. There are a few special cases in plants where the origin of new species has been observed. Whether or not it is practical to explain these cases to students will depend on their background in genetics and cytology and the time available.

A pattern that is relatively easy to understand involves the hybridization of two species followed by an accidental doubling of the chromosomes in the hybrid. The hybrid plant will possess one haploid set of chromosomes from one species and another set from the other species. This quite often gives an individual that is robust and excellent in all ways—until the time of reproduction arrives. Normal ova and pollen can be produced only if there is normal pairing of chromosomes in meiosis. Normal pairing can occur only between homologous chromosomes and the hybrid will possess different chromosomes from the two parent species. The result is meiotic chaos and generally abnormal gametes (this is the mule's problem).

If, however, there was an accidental doubling of the chromosomes, the hybrid would have all of its chromosomes in homologous pairs and meiosis could be normal. It would have the tetraploid number of chromosomes, which would make it difficult to be crossed back to the parent species.

This is more than a hypothetical model. There are many well studied cases of two species crossing, the chromosomes of the hybrid doubling, and the result being a new species—all in a season, instead of 200,000 years. One classic case is *Spartina townsendii* (Huskins, 1931). For other cases see the second edition of Dobzhansky's *Genetics and the Origin of Species* (pp. 231–242), Stebbins (1977, pp. 186–191), and M. J. D. White (1978, ch. 8).

Although geographic speciation appears to be the dominant mode of speciation, there are other less well documented possibilities. Bush (1975) and M. J. D. White (1978) can be consulted for details. It would seem better not to consider these other cases in a first-year course—we must accept that everything cannot be covered so the emphasis must be on the ubiquitous and important and not on the rare and important or ubiquitous and unimportant.

Molecular evolution

Today the study of evolution with the procedures of molecular biology is a very active field of research. The elegance of its probes, the rigor of its methods, and the precision of its answers are making it possible to gain deeper understanding of the processes of evolution. Molecular evolution is also an area where teachers of first-year courses must exert discipline and self-restraint. There will be a desire to open the eyes of students with a heavy dose of molecular evolution but we must face the fact that few students will have the background to understand why the new discoveries are so important and exciting. Neither will there be time to provide an adequate background. Unless there is restraint, it is more likely that the students' minds will become clogged by unappreciated facts than that their eyes will be opened.

Possibly the most practical course to adopt is to attempt to give students an indication of the sorts of questions that the techniques of molecular biology can answer.

The study of evolution at the molecular level is the study of the fundamental molecules of evolutionary change—DNA—and the molecules that represent the immediate products of DNA—the proteins. When one compares the bones of a horse and human being and then their hemoglobin molecules, the methodology is basically the same—comparing structure. The hemoglobin molecules, however, are immediate consequences of gene action whereas the bones are the consequences of complex interactions of cells and their molecules extending over the long period of embryonic development. Proteins are basic; bones are derivative.

Genetic variability. The traditional meth-

ods for detecting the number of alleles of a locus was laborious since it usually depended on genes that produced visible effects and on making a very large number of crosses. Furthermore, if radiations and other mutagenic procedures were used, one could hardly claim that heterozygosity under natural conditions was being studied.

Now we have electrophoretic techniques that enable one to detect differences in proteins—which reflect differences in the genes controlling them. Before these techniques were available, it was assumed that a low level of polymorphism would be normal. Now we know that in human populations about 30 percent of the loci are polymorphic and in any one individual about 7 percent of the loci are heterozygous. The values for other animals are similar.

Relatedness of organisms. The procedures of classical evolutionary biology for estimating relatedness were crude. Hybridization was one. Among similar species, if A and B could be hybridized but neither could be crossed with C, it was assumed that A and B are more closely related to each other than either is to C. If hybridization was impossible, then one had to rely on comparisons of structure—the closer the structural similarity the closer the relatedness and, presumably, the shorter time interval since a common ancestor.

Now it is possible to make detailed comparisons of the base sequences of different DNAs. This does not measure what genes do, merely whether or not their base sequences are similar. When different species of frogs or flies are compared, the sequences are the same for about 81–89 percent of the DNA. Two species of mice may have 95 percent of their sequences the same. A real surprise (shock?) is to learn that the base sequences of human beings and chimpanzees are at the 99 percent level. Whereas the fly species belong to one genus—the same is true for the species of frogs and of mice—we have placed the chimp in a separate family.

Similar experiments, comparing amino acid sequences of many different vertebrates, reveal that human proteins resemble those of other primates closely and, this resemblance of proteins decreases in the following order: rodents, dogs, marsupials, monotremes, birds, and amphibians. This is the same sequence that evolutionists had proposed, on other evidence, before molecular comparisons were possible.

If we take the paleontological estimates for the time when various groups diverged and add the data on molecular differences, we can then make an estimate for the rate of evolution of molecules. One estimate is that there are about 75 amino acid substitutions in protein molecules in 100 million years. In cytochrome c there have been about 25 amino acid substitutions in 500 million years. Human cytochrome c consists of 104 amino acids.

The field of molecular evolution is now in a period of validation. Its discoveries are in accord with what previous methods have established as the major concepts of evolutionary biology—we would be in serious trouble if that had not been the case. The main contributions of molecular evolution to date have been to give more detailed, and often more precise, answers to important questions. This evaluation will surely seem dated in the near future—the possibilities of gaining very much deeper insights into the mechanisms of evolutionary change with the methods of molecular biology seem endless.

For general introductions to the literature, see Nei and Koehn (1983), Rose and Doolittle (1983), Calder (1973), Ayala (1976), Dickerson (1980), Jukes (1966), and Zuckerhandl (1965).

Evolution and human welfare

Compared with the span of human life evolution is generally an exceedingly slow affair and hence might be expected to be of little immediate importance. This is not the case. Evolution impacts our food supply, health, educational system, social interactions, and even plans for our future. Evolution is much more than the study of dry bones—it is an ever present threat and promise for the human species.

Some of the ways that the concept of evolution, or the processes of evolution, are of immediate human concern will be listed briefly and references provided. There will be considerable overlap with

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topics that could also be dealt with when genetics is discussed. This is not surprising since genetics is short term inheritance and evolution is long term inheritance. Some topics, such as race, are more appropriately treated as an aspect of genetics and will not be included here.

Few studies of history attempt to deal seriously with the ways evolutionary principles relate to human beings. C. D. Darlington (1969) made such an attempt.

Agriculture

Human life can be sustained only by the death of other lives. Over most of the time span of our species, we depended on wild animals and plants for the substance and energy required to maintain our lives. Civilization became possible after the Agricultural Revolution of Neolithic times when our ancestors began to alter the evolution of a few wild species. Animals and plants were domesticated and selected for those characteristics that would be of immediate benefit to human beings—generally better food and fiber.

Some general references are Angress and Reed (1962), Baker (1970), D. and P. Brothwell (1969), Cohen (1977), de Candolle (1886), Grigg (1974), Heiser (1973), Helbaek (1959), Reed (1959), Sauer (1952, 1969), Singer *et al.* (1954–1958), Ucko and Dimbleby (1969), Vavilov (1951), and Zeuner (1963).

Much is known of the evolutionary history of important crops such as wheat and corn. Some key references are Beadle (1970), Jugenheimer (1976), Poehlman (1979), Peterson (1965), Chandraranta (1964), Higgs (1972), and Scientific American (1970).

Evolutionary principles become apparent when artificial selection is practiced. In natural populations there is tremendous genetic diversity and this is vital in allowing the population to respond to new environmental challenges. When human beings start to select plants and animals they concentrate on greater productivity or some other feature of benefit to man, not the species being domesticated. The inevitable consequence of this selection, which almost always involves close inbreeding, is to eliminate a large part of the natural genetic variability. This has two main disadvantages: the domesticated species might not be able to develop resistance to a new disease or to environmental stress and, should one wish to select for some other characteristic, the necessary genetic variability might not be available. Genetic uniformity of domesticated animals and plants might be desirable for the moment but, in the long run, it can be a disaster.

There is a fascinating vignette of evolution in action in the case of wheat and wheat rust. Plant breeders are constantly selecting new strains of wheat that are resistant to the rust. The problem is that the wheat rust is always evolving in ways that will allow it to flourish on wheat. Thus, there is a race between the natural evolution of the rust and the artificially directed evolution of the wheat (Stakman and Christensen, 1946; Stakman and Harrar, 1957, pp. 499–509).

For two good introductions to the evolutionary aspects of domestication see Day (1977) and Horsfall and Cowling (1980). Additional references are Wade (1972), National Research Council (1972), Feldman and Sears (1981), Lewin (1982), Strobel (1975), Hooker and Saxena (1971), Maugh (1982), Holton (1959), Caltagirone (1981), Stevens (1974), van der Plank (1968), and Maxwell and Jennings (1980).

A similar principle of evolution comes into play in human efforts to control insects and other pests of domesticated animals and plants. The pests are usually able to evolve resistant populations. Control, therefore, is a contest of human ingenuity and the ability of the pest population to evolve rapidly and effectively. See Brown (1971) and Georghiou (1972).

Health

Many human health problems are a contest between the speed with which disease organisms can evolve to live on us and we can evolve resistance, a long term affair, or invent ways of controlling the disease organisms.

Long ago, when human populations tended to be isolated, each evolved a degree of resistance to the endemic disease-pro-

ducing organisms, thus permitting survival of the population. The inhabitants of Western Europe had been selected by the organisms causing measles, scarlet fever, smallpox, and a host of other ills. During an epidemic many would die but the survivors tended to be somewhat more resistant and by the 18th century few of the diseases were serious threats to the lives of most members of the population. When Europeans began to colonize other continents they came in contact with native populations that had not evolved immunity to the diseases of Western Europe. The consequences could be devastating. The native Americans were conquered more by European disease than by European arms. See McNeill (1976, 1980), C. D. Darlington (1969), P. T. Baker (1960), Haldane (1957), and Fenner (1970).

The sickle-cell gene is widely distributed in Africa. When homozygous it causes severe anemia and usually early death. When heterozygous it affords considerable protection against malaria but causes a mild anemia (Livingston, 1958; Motulsky, 1960). Thus the human population in malarial regions has been selected for the resistance conferred by the sickle-cell gene.

For the general problems of the evolution of resistance in disease-causing organisms and the human response see Livingston (1960), Motulsky (1960), Friedman and Trager (1981), Elliott (1973), and Black (1975).

The concurrent evolutionary races of man and his prey and predators is what Van Valen (1973) calls the Red Queen Principle. Even as Lewis Carroll's Red Queen had to keep running just to stay in place, interacting natural populations have to keep evolving with respect to one another or become extinct. This is one of the fundamental facts of life. Every population of heterotrophs must continually evolve better ways of preying on other organisms and evolving better ways of avoiding being preyed upon. The pressures may be less for the photosynthetic and chemosynthetic organisms. They need not evolve predatory mechanisms—their main problem seems to be to avoid being eaten. We are only now beginning to realize the huge number of chemicals produced in our food plants that are carcinogens or mutagens (Ames, 1983). Inconvenient for us, perhaps, but these chemicals represent the plant's attempts to avoid being eaten.

Genetic engineering

The French biologist, Jacques Monod, entitled a book *Chance and Necessity* (1971). By this he meant that our evolution to the stage of *Homo sapiens* was based on chance mutations that were selected if they were necessary for the survival of our ancestral populations. Darwin would have approved of this title.

For three and a half billion years the course of life has been guided by chance and necessity. In the last 0.003 percent of this biotic era human beings have purposefully altered the evolution of some species of plants and animals by changing the "necessity." Necessity was no longer defined as "necessary for the organism" but "necessary for mankind." In addition we have inadvertently altered the evolution of many other species by our modifications of the environment. Melanic moths and weeds are examples.

Now we are on the threshold of an era of far greater power that will see us able to mold the genetics of species. We are still unable to control the specificity of mutation—it is still governed by that chance of Darwin and Monod. We are able, however, to transfer a desirable gene from one organism to another in some situations and it is reasonable to predict that the number of situations will increase rapidly. This is the field of genetic engineering.

Less than a decade ago there was a fierce debate involving scientists, political leaders, and the public about the risks of entering this new era. Some of us were terrified by the possibility of a new devastating pathogen, the product of directed genetic recombination, escaping from the laboratory and causing an epidemic that the medical profession would be powerless to control. But it was also realized that this new technique, which could produce disaster, could also produce marvels—bacteria made to synthesize insulin and other human hor-

mones; nitrogen-fixing genes to be introduced into plants. The possibilities for producing worthy results seemed endless. Grobstein (1977) discusses these early fears and prospects.

As the months went by the dangers seemed to be far less and the prospects far better. And there is always that subtle force: if something can be done, it will be done. Now genetic engineering is here to stay. The flow of information in this area has reached flood proportions. Most issues of *Science* and *Nature* have articles dealing with it. Frequent mention is made in the weekly news magazines and newspapers, even in the *Wall Street Journal*, because genetic engineering is a volatile growth industry.

One can enter the literature of the field via Cohen and Shapiro (1980), Villa-Komaroff (1980), Diacumakos (1981), and the entire 11 February 1983 issue of *Science* (vol. 219, no. 4585).

My advice for treating this topic in a first-year biology course will probably not be taken but here it is.

One cannot overemphasize the importance of genetic engineering for our future welfare. Many things are possible now and, at the current rate of progress, nothing seems theoretically impossible to accomplish. Therefore, we will be in a position to make decisions about ourselves and other forms of life never possible before. These decisions will deeply involve questions of ethics and the well-being of mankind and other forms of life. Decisions will be made and they must be made by informed minds.

It is most unlikely that students in a first-year course can master the technical aspects of genetic engineering—the necessary scientific background could not be obtained in the time that could be allowed for the subject. But is that background necessary? I think not. An efficient solution might be to provide students with information about the sorts of things that can be done and, as examples, provide a non-technical explanation of one or more of the simpler procedures: an example would be the transfer of a desirable gene to a plasmid and then to a bacterial cell where it could synthesize insulin or some other medically important substance.

If students become aware of the possibilities in genetic engineering they will be in a position to consider the implications—and that is the critical issue. One does not require an M.D. degree in order to hold a useful opinion about the delivery of health care in America.

Human evolution

Our lineage has been evolving for more than three billion years but for many students the main interest is in the last few geological moments—when our line became primates and then species of the genus *Homo*. This has been one of the more interesting but surely the most contentious field of biological research. It has involved international politics (whatever happened to Peking man? see Shapiro, 1974), intense rivalry among scientists (Johanson and Edey, 1981), fraud (Weiner, 1955; Oakley and Weiner, 1955; Gould, 1983, chs. 16–17), and has caused severe reactions by the fundamentalist religious sects (references shortly).

The subject is surely worthy of a lecture or so. Some useful references are: Scientific American (1967, 1979*b*), Pfeiffer (1969), L. B. S. Leakey and Prost (1971), Campbell (1972, 1976), Trinkaus and Howells (1979), Johanson and Edey (1981), R. E. Leakey and Lewin (1977, 1978), Howell (1973), LeGros Clark (1978), Pope (1983), and Rukang and Shenglong (1983).

The *Origin* makes only the most tentative statement about our evolution: "Light will be thrown on the origin of man and his history" (*Origin*, p. 488). Darwin knew of no fossil remains that threw light on our origins. Huxley's famous essays of 1863, *Evidence as to Man's Place in Nature*, made explicit the meaning of evolution for our history. Since there was no adequate fossil record (the first Neanderthal remains had been discovered in 1857 but Huxley found them difficult to interpret) he used the data of comparative anatomy, especially the close anatomical resemblances of man and the anthropoid apes, stone age artifacts, and observations on the "primitive" races still living. Some of the earlier attempts to throw light on our past history are Lyell

(1863), C. Darwin (1870), Lubbock (1869), Haeckel (1905), Joly (1891), Osborn (1916), and Keith (1931).

Students may be interested in the considerable artistic talents of prehistoric man: Breuil (1952), Bataille (1955), Graziosi (1960), Bandi (1961), and Leroi-Gourhan (1967).

Cultural evolution

It is worth emphasizing to first-year students that the human population is learning to circumvent some of the forces of natural selection. Modern medicine and modern agriculture mitigate the selective pressures of disease, malnutrition, and starvation. What we are and what we do are influenced more by cultural than biological factors. To be sure our culture may introduce new selective forces. We have so degraded our environment, adulterated our food, polluted our air and water, been lax in developing safeguards for nuclear technology, and failed to secure peace, to the point where human beings are the main force of selection on human beings. One of our main selective challenges today is to survive the mutagens and carcinogens that we have pumped into the environment.

But cultural evolution could promote a different future—one in which we could overcome the selfish gene (Dawkins, 1976) and emphasize love rather than Love Canals.

Cultural evolution is a vast subject. For a start try Dobzhansky (1962, 1973*b*), Dubos (1955), Comfort (1966), Campbell (1966), Washburn and McCown (1978), and Ardrey (1976). For more quantative studies see Cavalli-Sforza and Feldman (1981) and Cavalli-Sforza *et al.* (1982).

The creationist phoenix

Much of the initial opposition to the Darwinian paradigm was due to its obvious conflict with the creationism paradigm. In the middle of the 19th century, most of the Western World accepted as fact the Genesis account of the origin of the earth and its inhabitants. Numerous different stories about creation were to be found in other cultures but these other cultures were not active participants in scientific speculation. The acceptance of the Genesis account had been weakened to some degree during the Age of Reason but, as noted before, most scientists in 1859 were creationists.

In the years immediately after 1859, it was possible legitimately to oppose Darwinism on two counts: inadequate scientific evidence and heresy. Later research supplied the scientific underpinnings but the charge of heresy will always remain—the concept of evolution is in direct conflict with a literal interpretation of Genesis. But this is heresy only in the minds of the fundamentalists. The major religions have accepted evolution and made whatever philosophical adjustments were required.

Huxley was the most notable defender of evolution in Darwin's lifetime and many of his published essays (1893, 1895*a–f*) are concerned with this subject. The literature of the field is immense. Useful accounts are Eiseley (1958), Glick (1972), J. C. Greene (1959), Hofstadter (1963), Hull (1973), Irvine (1955), Kogan (1960), Moore (1978), Ruse (1981), Russett (1976), Turner (1974), and R. J. Wilson (1967).

The creationist movement waxes and wanes. The current expression of it seems to have peaked last year and is now less in the news. Nevertheless it remains a serious threat to the teaching of science and, by extension, a threat to all freedom of teaching. The creationist challenge to science teaching and its pressures for "equal time" have been dealt with by Nelkin (1977, 1982) and Moore (1975, 1982).

The recent resurgence of creationism is part of a worldwide shift to fundamentalist religions. In the United States there has been a vigorous response by the scientific community. See Futuyma (1983), Newell (1982), Ruse (1982), Kitcher (1982), Zetterberg (1983) and the entire January 1982 and March 1983 issues of the *Journal of Geological Education.*

The problem of evolution vs. creationism does not involve science in any serious manner but it is an important intellectual and social issue. In view of the great confusion that exists in the minds of the majority of Americans it should be considered in first-year university courses. It is,

obviously, a delicate question for some schools and some parts of the nation. The goal of any discussion must not be to persuade religious believers to be non-believers but to show the differences between statements based on scientific information and those based on any of a number of religious belief systems. The claims of some of the more vocal creationists that there are scientific facts that support creationism and falsify the concept of evolution are simply not true—though these claims may gain credence with the general public by constant repetition.

The question of why some people prefer to accept creationism rather than science is interesting but, surely, not of concern to teachers. In the United States people have a right to believe as they wish with or without evidence. They do not have the right, however, to pressure others to conform to whatever sectarian views they may hold. I have tried to analyze this problem (Moore, 1983).

Schedules

Although this long essay forms a unit, it is not intended that evolution be taught as a unit in a first-year biology course. If the concept of evolution is accepted as the grand unifying theme of biology, it should permeate the entire course. My suggestions for scheduling the various topics follow.

Deductions 1–10, plus "Was Darwin right?" form a unit that gives the fundamental concepts of the field and an understanding of the evidential basis for the concepts. This could come early in the course and in association with laboratory exercises designed to illustrate organic diversity.

Deductions 11–15 are intended as examples of the leitmotif that can accompany consideration of all the major subject areas of biology.

The section "Evolution after Darwin" is suggested for late in the course and certainly after cell biology and genetics have been covered.

The topics listed under "Evolution and human welfare" could be treated as a unit or, better, I think, be distributed throughout the course. There are many other topics of this nature that could be developed.

Concluding remarks

I believe that the time has come to accept the fact that the concept of evolution is the unifying theme of the biological sciences and what is taught in the first-year course should reflect this point of view. The main purpose of the ASZ project, however, is to suggest ways for improving biology teaching at the college and university level. There seems to be a gnawing feeling among those concerned with higher education that our problem is not so much what we teach but how we teach. The strategy suggested here is that we should reduce the factual load and give greater attention to the conceptual framework of the field. It is surely true that students can learn far more than they understand, but to what purpose? There are difficulties with the suggested approach. It is far harder to teach concepts than facts and most of our students' prior education will have dealt more with facts than ideas. Concern for ideas does sound elitist but we simply have to accept that higher education is an elitist enterprise. The style of education must be set for those who wish to learn and understand and not by those unable or unwilling to so do. The enjoyment of ideas, like the enjoyment of beer, seems to be an acquired characteristic—and not everyone likes beer.

There are other pressures that make teaching in a conceptual mode more difficult. First-year biology courses are usually very large and for this reason objective-type examinations seem to be the rule. One must accept from the onset, I believe, that it is pointless to attempt to teach concepts and then test for facts—as objective examinations do almost exclusively. Students will not be persuaded when you tell them that the important things they should learn are the "big ideas" when your evaluation of their success in so doing is to ask a question that can be answered by checking a letter A–D.

Another pressure comes from the premeds who tend to dominate many first-year courses. They believe that success for them means learning the maximum number of facts and, in this respect, they have learned to excel. The grades they obtain in science courses will depend on examinations that emphasize facts. The various

national examinations they will take in the screening processes for medical school also stress facts, although attempts to search the higher levels of the students' brains are under way. I have found premeds restive and on occasion hostile when there is a heavy dose of concepts followed by a testing of their understanding with essay-type examinations.

Then it must be admitted that some young instructors, who have just completed a fact-laden, concept-poor science curriculum of some universities, find the conceptual world neither familiar nor comfortable. They have been trained more as technicians than as scientists.

In spite of the difficulties, we must change the ways we do our teaching—for the health of the nation, the welfare of our students, and our own satisfaction. It is terribly important that we make these changes and it will be terribly difficult to do so. Teaching must return to a place of distinction and reward in the universities. This need not result in damage to research programs. Good teaching and good research are not incompatible. Ideally they should be synergistic.

Educational reform, the *sine qua non* for a viable future for our nation and for its citizens, must begin with us. We must help students acquire a deep understanding of the nature of science and its strengths and limitations. This goal is equally important for those who plan a career in science, become teachers of science in the schools, or make the informed decisions of a democracy.

A course in science must be an intellectual adventure. What is known is ephemeral. Science as a way of knowing is forever.

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